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CHEMISTRY AND THE MODERN MEAT PACKING INDUSTRY

MINARD PATRICK*

Received May 15, 1938; published August 25, 1938

FOREWORD

The subject, *Chemistry and the Modern Meat Packing Industry*, is in no wise a limited one. An initial consideration of the problem, however, is not likely to reveal the possibility of research that it ultimately affords. A more thorough study provides an open Sesame, so to speak, for the student interested in modern phases of chemical application. In fact, the topic in detail

* Editor's Note.—The following quotation from *Denison University Bulletin* (Announcement by the Department of Chemistry) Vol. 37, No. 18 (September, 1937) is self-explanatory. The thesis submitted by Minard Patrick is printed without corrections or changes.

"WOODLAND PRIZES IN CHEMISTRY. Under the terms of the will of J. Ernest Woodland two prizes have been established in memory of his father, William Henry Woodland. These prizes are to be awarded annually as follows:

"(a) One hundred and fifty dollars to the student, in full and regular standing in any course in Denison University leading to the degree of Bachelor of Arts or Science, who shall prepare under the direction of the head of the Chemistry Department of Denison University, and present at the end of his or her junior year, the best original thesis on some phase of chemistry in its relation to industrial or everyday life.

"(b) Fifty dollars to the student, in full and regular standing in any course in Denison University leading to the degree of Bachelor of Arts or Science, who shall prepare, under the direction of the head of the Chemistry Department of Denison University, and present at the end of his or her junior year, the second best original thesis on some phase of chemistry in its relation to industrial or everyday life.

"The purpose of these prizes is to stimulate a wholesome interest in the practical applications of the science of chemistry.

"For 1937–1938 the subject of the thesis is *Chemistry and the Modern Meat Packing Industry*.

"Students contesting for these prizes must register formally with the Department on or before November 15, 1937, and theses must be submitted in final form on or before May 15, 1938."

becomes so broad that one could not hope to present a complete review of it in less than a few dozen volumes.

Therefore, my problem, instead of being one of elaboration upon a single phase, has been to give a general conception of the whole of the industry, stressing important and typical chemical reactions. I have minimized mechanical processes, interesting and valuable as they may be, in order to adhere to the topic at hand. Historical evolution, rhetorical presentation, and style have been placed secondary to technical exactness in this thesis, for it is my belief that the original purpose of a work of this type should be informative in nature.

My aim has been to present a readable paper—not so technical as to incur the apprehensions of the layman, and yet advanced enough to show intelligent thought and understandable theory. Wherever possible I have visited plants in operation and conferred with the chemists employed there in order to substantiate and revise information obtained from library research. I have endeavored to present methods in most recent practice; however, it is often very difficult to learn of the latest processes because they are so closely guarded by wary owners. For this reason it is often impossible to obtain information on methods that have been employed less than a year or two.

I have eliminated sausage from the discussion, not because chemistry is not involved, but because so much has to be said on the subject before any definite conclusions can be reached. That the product is interesting is granted, but that much valuable information is gained from its study is doubtful.

In addition to sausage, there are numerous other by-products that might have been mentioned; in the main, however, I have selected the products of chief concern in everyday use and that are most interesting from a chemist's point of view.

There is no doubt that the problem at hand is a good one. It gives a typical example of an industry that has been developed into a leader in the nation, primarily through the creation and utilization of the numerous by-products by chemical accomplishment. What we may expect in the future is only problematical.

It would seem that we have approached a veritable millennium in this business; but, on the other hand, wouldn't we have said the same thing two decades ago? Thus, we can never be certain what the future has in store. Perhaps in fifty years, the development of the meat packing industry up to the year 1938 may seem very primitive to our grandchildren.

My indebtedness to individuals who have shown me numerous kindnesses during my preparation of this thesis can be acknowledged in no adequate manner. I am especially grateful to Mr. H. W. Lawrence, head of the Norwalk High School chemistry department; Mr. N. B. Betzoldt, superintendent of Durkee's oleomargarine plant; Dr. Harvey, head of research for Wilson and Co.; Mr. Russell Smith, head of Wilson's dog food department; Mr. G. Mottelson, superintendent of Wilson's pharmaceutical laboratories; Mr. Arthur Guillidiu, Swift's fats and oils department; Mr. M. M. Piskur, Swift's librarian; Miss Bertha M. Butler, Norwalk librarian; and Miss A. L. Craigie, Denison University librarian.

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> Why does this magnificent applied science which saves work and makes life easier bring us so little happiness? The simple answer runs: Because we have not yet learned to make sensible use of it.
>
> —Albert Einstein.

Part I. Meat

Chapter I

Meat Preservation and Curing

From pioneer times one of the greatest problems that have faced the meat packer is how to prevent spoilage of his chief edible product—meat. Since meat is not chemically stable at ordinary temperatures, nor is it free from the ravages of the microscopic parasites that we know as bacteria, the packer must resort to some means of control. With the introduction of modern methods of technique and chemical and engineering practice, however, the problem has evolved into a huge research experiment with new operations and variations of technical procedure constantly supplanting out-dated methods. In this large field of research the chemist of today plays a leading rôle.

There are several contributing factors toward the spoiling of meat. One of these is the natural presence of digestive enzymes that break down the tissues by a process of self-digestion, called

"autolysis". Putrefaction, the principal cause of deterioration, results from the action of molds, yeasts, and bacteria which thrive on food of an organic nature. Meat is especially prone to attack since moist proteins provide excellent food for bacteria. Rancidity in meats is due essentially to oxidation of residual fatty tissue into aldehydes and lower fatty acids, which are characterized by their foul odors.

There are four methods in common use of preventing spoilage of meat—namely, refrigeration, heat sterilization and canning, desiccation, and curing; the latter includes chemical preservation and condimental treatment.

Refrigeration, or "chilling", as the packer calls the process to distinguish it from outright freezing, is, of course, the most prevalent method of preserving meat. Animal heat, which is actually no different from any other form of heat, must be removed from the freshly-slaughtered carcass as quickly as possible, since moisture and warmth are greatly conducive to bacterial growth. Preliminary cooling is carried on at a temperature just above freezing, 34°–36°F. The maintenance of this temperature until shortly before cooking is highly desirable. During this operation meats lose moisture amounting to about two to two and a half per cent by weight. This loss is termed "chilling shrink".

"The several factors which determine the changes that take place during freezing and thawing may be summarized as follows:

1. The pretreatment—the temperature conditions in the carcass at the time of freezing, together with the time interval that has elapsed between slaughter and freezing.
2. The lowest temperature attained and the changes in the temperature while in the frozen state.
3. The rate of freezing.
4. The mode of thawing." (28)

Frozen meats have recently been brought to public notice more than formerly. New processes and advanced study of biological changes and control of these changes have been instrumental in bringing quickly frozen meats to the fore. Beef frozen in brine becomes brown in color. Chemically, the change is

from hemoglobin, red coloring matter found in organic substances, to methemoglobin.

Desiccation, or drying, of meats is of relatively little value in meat preservation except as a means of transporting meat under unusual circumstances. Drying depends for its success in preservation upon the loss of a large percentage of water from the meat, especially from the surface. Microörganisms need moisture for their reproduction; hence, if the surface of the meat is sufficiently dehydrated, putrefaction is considerably hindered. Dried, or "jerked," meat is not commercially important. It is less palatable and digestible, and has a lower nutritive value than other meats. The heat of drying tends to coagulate some of the proteins and accordingly changes the composition to some extent.

A means of keeping meats indefinitely is by cooking and canning. Cooked meat, of course, keeps longer than fresh meat because during the process, harmful microörganisms are nearly completely destroyed; temperatures between 131°–158° F., called "pasteurizing temperatures," are usually sufficient to kill all bacteria.

Curing meat involves the application of such preservatives as common salt, sugar, wood smoke, vinegar, spices, salt-peter, sodium nitrate, and sodium nitrite. These preservatives may occur alone, but more often are present in various definite proportions in the finished cured product. A few other compounds are sometimes employed, but are usually classified as adulterants,[1] since they are likely to produce a poisoning effect on the consumer. According to Moulton (28) there are six characteristic methods of curing meat. These include dry-salt curing, pickling, sweet pickling, box curing, corning, and dry curing. Of these

[1] It is known that fraudulent manufacturers sometimes use substances which inhibit change in appearance of meat, but do not prevent bacterial growth. For example, sodium sulfite will restore and retain the red color of fresh meat even though the meat may have long since passed the point of being acceptable as edible food. It is evident that meats treated in this fashion are even more harmful than if they had received no treatment at all. In recent years, however, careful government restrictions upon preservatives in foods have reduced these practices to a minimum.

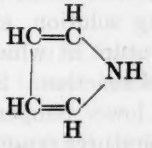
methods, dry-salt curing and pickling are perhaps the most important.

Sodium chloride is the chief curing agent used in nearly all methods. Salt, in certain concentrations, tends to discourage bacterial growth. Of course, salt is not toxic to all micro-organisms, but it does combat satisfactorily the certain kinds that attack meat. Sucrose (sugar), the next most common curing ingredient functions as a flavoring constituent rather than a preservative in the true sense of the word. In higher concentrations sugar is valuable in preserving foods, but it is doubtful whether concentration is sufficient for any noticeable preservative value in curing solutions. Spices, except in highly spiced meats popular with foreign trade, exert primarily a flavoring influence. Vinegar, which also adds flavor, incidentally, has a definite nullifying effect upon bacterial reproduction. This is doubtless due to its acid properties.

Sodium nitrates and nitrites, as well as potassium nitrate (Chile saltpeter), have been used for some thirty years now as color-fixing agents, giving meats their healthful, palatable appearance. The chemical reaction that occurs Moulton explains by the following outline:

"Nitrate + reducing-bacteria gives nitrite. Nitrite + hemoglobin (red coloring matter of meat) gives nitrosohemoglobin (red coloring matter of cured meat). Nitrosohemoglobin + heat gives nitrosohemochromogen (red coloring matter of cooked cured meat.)" (28)

Hemoglobin, according to a standard organic chemistry text (17), is a combination of four pyrrole nuclei:



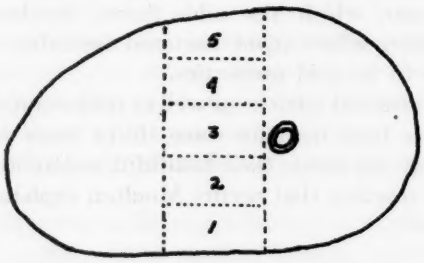
Evidently biological chemists are still undecided as to the definite structural formula of this pigment which gives our blood its characteristic color. Nitrosohemoglobin is the compound ob-

tained by replacing the hydrogen atom directly attached to the nitrogen atom by an $-N=O$ group.

The nitrite and nitrate are used in ratios varying from 1:3 to 1:10 respectively. The aqueous solutions of these salts are known as "curing-pickles." Analyses are constantly being made of hams in various stages of cure, as well as the pickle itself, for determination of specific gravity, and nitrate, nitrite, sugar, and salt content. The following figure shows how hams are divided into sections from which the samples for analysis are taken. Number one is the fat side, number five is the flesh side,

I

Diagram of Method of Sampling Hams (26)



and number three is termed the middle piece. By these determinations, the coefficient of variability of salt content can be ascertained, which is a "numeric" expressing the distribution of the amount of salt present. A nearly equal distribution, which is to be desired, of course, makes this value small.

Several factors must be considered in brine curing—namely, the strength of the curing solution, effect and distribution of pumping solution, temperature at which the reaction is carried out, and length of time of reaction. Satisfactory temperatures range from 34° to 36°F., lower temperatures tending to retard the cure and higher temperatures tending to encourage spoilage. The time of curing usually runs about three or four days per pound depending upon existing conditions. After soaking in brine the required time, the meats are allowed to soak in water to

reduce the percentage of salt in the exterior portions of the cut. The meats are then smoked[2] and stored.

A method for calculating salt content which is a practical application of the method of chloride determinations taught in college quantitative analysis courses is given in a government pamphlet (26):

"A 5-gram sample of the ground meat was weighed into an Erlenmeyer flask, and to it were added an excess of one-tenth normal silver nitrate, 10 cc of saturated potassium permanganate solution, and 25 cc of concentrated nitric acid. This mixture was boiled vigorously until all solid particles of the meat were completely digested, the average time required being about 20 minutes. Perforated glass beads were used to prevent bumping during the digestion.... When cool, the excess of silver nitrate was titrated with potassium thiocyanate in the presence of 2 cc of saturated ferric alum and 10 cc of acetone. By having a total volume of not more than 100 cc, an easily distinguishable brownish-red end point was obtained without filtering off the white precipitated silver chloride from the yellow solution resulting from the digestion. A blank determination on fresh pork showed it to be so low in chlorine so as not to influence the results obtained in this study, in which relatively large quantities (about 7% of dry matter) of salt were present."

Dry-salting is the simplest method of curing known and is found to be highly satisfactory. Usually the cuts of meat are first dipped in brine to moisten the surface and then rubbed with a variation of the mixture of salts used in pickling. In time this salt mixture penetrates to the center of the cut by diffusion. A common curing mixture is eight pounds of sodium chloride, three pounds of brown sugar, and three ounces of saltpeter. (Nitrite may or may not be used.)

"Box-curing" is a variation of "dry-salting" in that the meats are salt-packed tightly in boxes; box-curing is the usual process in producing fancy bacons.

Canned corned beef and dried beef are well known products typifying two other methods of curing previously mentioned.

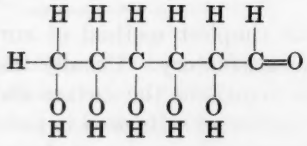
[2] By experiment, the best woods for smoking—that is, those that impart the best flavor to the meat—are oak, maple, hickory, beech, and juniper.

The curing agents are practically the same as those used in pickling, but exist in different proportions. Mechanical processes are, of course, essentially different.

Sweet pickled meats are prepared similarly to brine cured; however, as might be expected, sugar occurs in greater proportions and a syrup or honey is added to the solution. The familiar "sugar cured hams" that one sees advertised in eating houses and meat shops are products of this method of curing. It is estimated that over 30,000,000 pounds of sugar are used annually in curing meats.

During the World War, when sugar was at a premium, a pressing problem of packing house chemists was to find suitable substitutes for sucrose that would maintain the high standard of their product and still be financially feasible for use. To this end, extensive experiments were conducted on a number of sweetening agents that might be readily available. Among the materials found to be satisfactory in most instances were dextrose, cerelose, 70 per cent corn sugar, and refiners' sirup.

Dextrose is one of the most common of the so-called "hexoses," or six-carbon sugars. It is also familiarly known as glucose, and grape sugar. Its structural formula is



showing the presence of the aldehyde group ($-CHO$) and the OH groups which give the characteristic sweet taste.

Cerelose is the commercial name of a very pure crystalline monohydrate chemically like dextrose both in composition and function.

Seventy per cent corn sugar is a crude product which contains approximately seventy per cent dextrose, twenty per cent moisture, six-tenths per cent ash, and the rest dextrin.[3]

[3] Dextrin is an intermediate colloidal substance formed during the hydrolysis of starch.

Refiners' sirup is a dark-brown, strong-flavored liquid of variable composition and is a resulting product from cane sugar refining.

Thus it is that the preservation of meat provides employment for thousands of chemists, biologists, and bacteriologists. To attempt to give a complete synopsis of the tests they carry out and the discoveries they report would necessitate several volumes of facts and figures. However, from a general consideration of the subject, we may recognize the importance of this vast industry, which helps to feed the nation.

II

Percentage Composition of Some Kinds of Lean Flesh (2)

	OX	CALF	PIG	HORSE	FOWL
Water	76.1	75.6	72.6	74.3	70.8
Proteins and gelatin	20.0	19.4	19.9	21.6	22.7
Fat	1.5	2.9	6.2	2.5	4.1
Carbohydrates	0.6	0.8	0.6	0.6	1.3
Salts	1.2	1.3	1.1	1.0	1.1

III

Percentage Returns from Animal (16)

	% FROM MEAT	% FROM BY-PRODUCTS	% FROM HIDE
Hog	96.6	3.4	Sold with carcass
Sheep	81.4	4.1	14.5
Calf	92.8	7.2	Sold with carcass
Steer	87.3	4.1	8.6

IV

Weight of Steer Products (16)

	% GREEN PRODUCT	% OF FINISHED PRODUCT TO LIVE STEER
Beef	55.6	54.3
Shrinkage	6.8	6.8
Valueless materials	10.1	10.1
Additional shrinkage through processing	.....	11.6
By-products	27.5	17.2
Total	100.0	100.0

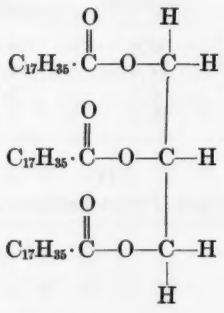
Part II. Derivatives of Fats and Oils

CHAPTER II

Fats and Oils in General

With the exception of protein food, lean meat, the most important products obtained from packing house processes are fats and oils. First let it be said that the essential difference between a fat and oil is one of physical condition; that is, the substance is known as a fat if it is a solid at ordinary temperatures, and as an oil if it occurs as a liquid. Desha (17) defines fats and fatty oils as "naturally occurring mixtures of triglycerides, most of which are of the mixed type."[4]

A glyceride is an ester of glycerol ($C_3H_5(OH)_3$) and one to three fatty acids (type formula R-COOH, where R is a hydrocarbon radical). A typical fat is stearin:



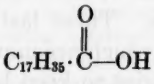
There are three main classes of human food—nitrogenous, or flesh-forming; carbonaceous, or energy-producing; and mineral. Fats, which belong to the carbonaceous group, are particularly valuable as energy producers. It can readily be seen that a fat would tend to produce more calories of heat upon complete oxidation than would a carbohydrate such as sugar ($C_{12}H_{22}O_{11}$), or

[4] In the broad sense of the word, an oil may be any liquid with a smooth unctuous feeling, insoluble in water, and less dense than water; however, in this discussion reference to oils will pertain to the glycerides spoken of above.

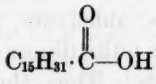
starch ($C_6H_{10}O_5$), for the reason that the hydrogen to oxygen ratio is considerably greater in the former.

Fats and oils are obtained from vegetable and mineral sources as well as from animals. When a fat is chemically pure, however, its source makes little difference in the use to which it is put. For this reason and others, many products, such as oleomargarine, are made of mixtures of animal and vegetable fats. Primitive methods of fat recovery were to heat up the fatty tissue from animals in open pans or kettles with little regard for cleanliness or economy. Modern rendering includes four recognized methods which will be described in connection with lard production.

A fat, as it is obtained from animal tissue, usually consists of a mixture of glycerides of saturated and non-saturated fatty acids. Typical examples of the saturated series are stearic and palmitic acids shown below:

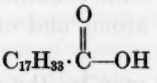


stearic acid

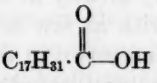


palmitic acid

An acid is said to be saturated when all the valence bonds in the hydrocarbon chain are completely satisfied. In the event of double bonds in the chain, the compound is unsaturated, or able to take up hydrogen atoms. Two common unsaturated acids found in fats and oils are oleic and linoleic acids:



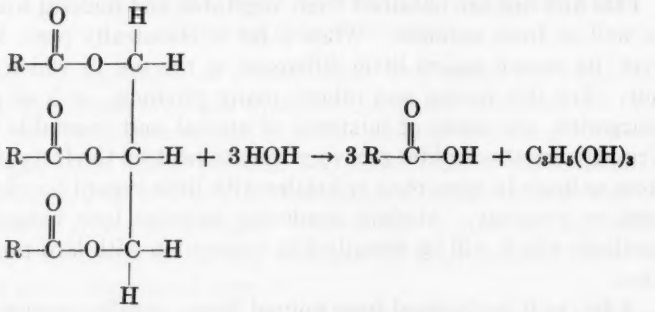
oleic acid



linoleic acid

When a fat is exposed to air at normal temperatures, two principal chemical reactions occur—hydrolysis and oxidation. The hydrolysis of a fat is exactly the opposite of esterification. In

the former process, the glyceride breaks up with the aid of moisture into three molecules of fatty acid and one of glycerin:



If the fat is a mixture of stearic, palmitic, and oleic glycerides, the corresponding acids are produced. Oxidation of a fat, by virtue of the splitting of the chain as well as other complex reactions, is likely to result in any number of different compounds, chiefly acids, aldehydes, and ketones. These last named substances have quite disagreeable odors which account for the odor of rancid fats. Thus, the producer tries to keep his edible fats and oils refrigerated up to the time of consumption. A fat that contains no excess of fatty acid is said to be "neutral."

It is very difficult to determine the composition of a fat, unless it is first hydrolyzed. Then a fairly accurate analysis can be made on the resulting fatty acids. An estimate by this method of the composition of average beef tallow is 25 per cent stearin, 25 per cent palmitin, and 50 per cent olein. Other common fats and oils vary greatly in composition, some containing fatty acid molecules with as few as six carbon atoms and others with as many as twenty-two in the chain.

The more unsaturated a compound may be, the more likely it is to be a liquid. In many cases the liquid form is highly undesirable; hence, a process called hydrogenation, which adds hydrogen to an unsaturated compound, has found great industrial use in hardening fatty oils. A typical hydrogenation reaction is shown herewith:

$$C_{17}H_{33}\cdot\overset{\overset{O}{\|}}{C}\text{—OH} + H_2 \rightarrow C_{17}H_{35}\cdot\overset{\overset{O}{\|}}{C}\text{—OH}$$

oleic acid — stearic acid

Although hydrogenation was first successfully carried out by Norman in 1903, the process did not come into prominent use until about fifteen years later. Since that time rapid strides have been made in the perfection of the method. One of the most ardent promoters of hydrogenation is Carleton Ellis, who

V

Classes of Fatlike Substances—Lipids (28)

1. a) Fats: neutral esters of glycerol and fatty acids solid at 20°C.—tallow
   b) Fatty acids—stearic acid
2. Fatty oils: neutral esters of glycerol and fatty acids liquid at 20°C.
   a) Drying oils—linseed oil, fat of the polar bear
   b) Semidrying oils—cottonseed oil, horse oil
   c) Non-drying oils—olive oil, oleo oil, lard oil
3. Essential oils: volatile and odoriferous substances of an oily consistency and varied chemical nature—oil of wintergreen, oil of peppermint
4. Waxes: esters of sterols and fatty acids—beeswax, sperm oil, spermaceti
5. Sterols: alcohols, generally of the terpene group, solid at ordinary temperatures—cholesterol, phytosterol, acetyl alcohol
6. Phospholipins: combinations of phosphoric acid and fatty acids—lecithin and cephalin
7. Glycolipins: combinations of fatty acids and a carbohydrate, generally glucose or galactose
8. Sulpholipins: combinations of sulphuric acid and fatty acids
9. Aminolipins: combinations of fatty acids and some amino-nitrogen-containing substance

has written several exhaustive volumes on the subject. The process is successful only under certain conditions and with the aid of suitable catalysts. The oil to be hydrogenated is placed in a tank that is heated by steam pressure and equipped with a mechanical agitator. Hydrogen gas is introduced through the oil while it is being heated and stirred under pressure. The catalyst is finely divided nickel or nickel oxide. As the hydrogen gradually enters the molecules, the oil becomes harder. By

experiment, it was found that the least saturated compounds were the first to absorb hydrogen, the apparent affinity for the gas decreasing with saturation. Thus the process is continued until the desired consistency is obtained. If cottonseed oil, for example, is being hydrogenated to obtain a synthetic lard, the reaction is stopped when the consistency approximates that of natural lard. Formerly the hydrogenation was carried out to completion and then, if the produce was too stiff, they would add a certain proportion of cottonseed oil. Unfortunately, the tendency of hydrocarbons to oxidize increases with unsaturation; thus, the difficulty in keeping these mixtures from becoming rancid led to the more modern method of partial hydrogenation, which has proved to be quite satisfactory.

Three important terms in the manufacture and sale of fats and oils are (*a*) free fatty acid content, (*b*) titer, and (*c*) M.I.U. Determination of these factors requires a trained analytical chemist.

Free fatty acid content, abbreviated F.F.A., is self explanatory in meaning. Fat in the animal body is neutral, but upon removal and in the presence of moisture, heat and enzymes, it will be partially converted into fatty acids as described before. Since free fatty acid is undesirable, a neutral fat will command a better price than carelessly kept products.

Titer is a term used in the determination of the hardness of a fat or oil. Since most of these substances are mixtures having indefinite melting points, the temperature at which the fatty acids solidify is taken as the titer. The acids are first separated from their glycerides by an alkali, such as sodium hydroxide. Oils have lower titers than fats, of course.

M.I.U. is the abbreviation for "moisture, insoluble matter, and unsaponifiable matter." A pure fat should have a very low percentage of these constituents. Moisture is determined by volatilizing a sample. Insoluble matter includes animal tissue and impurities that might have been introduced during processing. Unsaponifiable matter is the fat-like material that will not react with an alkali.

Iodine value is determined by the amount of iodine that an unsaturated oil will absorb. This determination is a satisfactory

indication of the number of double bonds a compound may have. Theoretically the process is analogous to hydrogenation.

Certain other tests are applied to some fats and oils to determine quality and deviation from standard. These include acetyl value (hydroxyl groups present), specific gravity, color, cloud test, flow test, smoke point, and others.

The table below gives a comparison of the composition of fat and protein. The latter is the chief constituent of lean meat.

VI

Percentage Composition of Animal Fats and Proteins (28)

SUBSTANCE	CARBON	HYDROGEN	OXYGEN	NITROGEN	SULFUR
Fat	76–77	11.6–12.0	11.0–11.6	None	None
Protein	50–55	6.5–7.6	20–24	12–18.4	0.3–1.9

VII

Some Uses of Animal and Vegetable Fats and Oils (28)

Product	Fats and oils used in manufacture
Lard substitutes	Lard, coconut oil, soy-bean oil, corn oil, cottonseed oil, oleo oil, animal stearine, vegetable stearine, peanut (Arachis) oil
Salad and cooking-oils	Soy-bean oil, corn oil, cottonseed oil, peanut oil, and olive oil
Oleomargarine	Neutral lard, oleo oil, animal stearine, cottonseed oil, corn oil, peanut oil, tallows
Margarine	Soy-bean oil, corn oil, peanut oil, cottonseed oil, and coconut oil
Animal stearine	Tallow, beef fat, and hog fat
Vegetable stearine	Peanut oil, cottonseed oil, corn oil, and soy-bean oil
Oleo oil	Tallow, hog fat, soy-bean oil, corn oil, cottonseed oil, and peanut oil
Neutral lard	Hog fat
Soap	Tallow, hog fat, fish oil, soy-bean oil, corn oil, cottonseed oil, peanut oil, olive oil, coconut oil, palm oil, and palm-kernel oil

The most important products that utilize fats as raw materials are lard, oleomargarine, and soaps. The production of these compounds will be discussed in succeeding chapters. Some other substances that are important but are too varied to include in full detail are vegetable oils, neatsfoot oil, lard oil and grease, oleo oil, and tallows.

CHAPTER III

Lard

Lard is a by-product of the meat industry that needs neither description of appearance nor detail as to use. This familiar cooking fat has been in use in American homes for many decades; there has never been a substitute that has successfully replaced lard, nor does it appear that a product, "just as good" will supplant it for many years in the future.

"Rendering" is a technical term which merely means the melting out of fat from fatty tissue. The following are the four principal methods of rendering employed in modern practice, with the respective products resulting from each method:

1. Low temperature dry rendering—neutral lard, oleo stock and oil.
2. Ordinary dry rendering—kettle-rendered lard, dry-rendered lard, dry-rendered tallow.
3. Steam rendering—prime steam lard, tallow, and grease.
4. Rendering by heating in water—head tallow, mutton tallow, neatsfoot oil.

Fats used in lard manufacture—that is, fats obtained from the hog—are known as killing and cutting fats. Killing fats are obtained from the interior of the carcass directly after slaughter; whereas, cutting fats are taken from the outside of the carcass after it has been chilled. The killing fat melts at a temperature of about 5°C. higher than cutting fat because it is maintained at body temperature during the animal's life; the cutting fat is more exposed to climatic conditions. For this reason it is necessary to make a mixture of the two kinds of lard that result for a product of correct hardness.

Lard manufacture is primarily a process of mechanical and engineering technique rather than one concerning characteristic chemical changes. Lard, however, does have complex chemical structure.

"Lard, like most natural products, shows wide variations in its chemical and physical characteristics, and this increases the difficulty

of basing definite conclusion as to purity on the results of analysis. . . . Lard consists principally of glycerides of stearic ($C_{17}H_{35}COOH$), palmitic ($C_{15}H_{31}COOH$), lauric ($C_{11}H_{23}COOH$), and myristic ($C_{13}H_{27}COOH$) acids, and of the liquid fatty acids, such as oleic ($C_{17}H_{33}COOH$) and linoleic ($C_{17}H_{31}COOH$) acids. The different physical properties of several samples of lard are due, in the main, to variations in the proportions of these different constituents." (16)

Steam lard, which comprises about 80 per cent of all lard manufactured, is the product of steam rendering. It is made by steam cooking the raw materials[5] in a cylindrical steel tank under a pressure of forty pounds. High quality steam lard made from fresh hog fat is designated as prime steam lard.

Kettle rendered lard has the best qualities for all cooking purposes. It is manufactured from the better grades of fat by heating them in a steam-jacketed kettle. Moisture is evaporated and the resulting lard is ready for use as soon as it has been properly strained to rid it of fiber.

Neutral lard is the product of careful low temperature rendering, hot water being used in the kettle jackets instead of steam. This product must be practically flavorless, for it is used almost solely in the manufacture of oleomargarine.

It is usually necessary to purify prime steam lard after it has been rendered. The first step is to remove all excessive water by settling or by artificial separators. After dehydration, the lard is bleached with fuller's earth and filtered through a filter press. An intermediate process to increase heat resistance and prevent separation is often applied. This consists in passing the hot melted lard over a revolving, refrigerated steel cylinder called a "chill roll." The lard is then scraped off in a semi-solid state and mechanically beaten to assure a smooth product.

Hydrogenation, a process previously explained, has been used considerably in recent years to harden lards of too low melting point. In this connection, synthetic lards, made from refined peanut oil and cottonseed oil, are hardened to proper consistency by hydrogenation.

[5] The raw materials in steam rendering are poorer quality (tissues, bones, etc.) than are used in other methods.

CHAPTER IV

Oleomargarine

Oleomargarine is the name given to butter substitutes in this country that are made by churning fats other than butter fat with milk or cream to form an emulsion.

Margarine, as the product is popularly but illegally called,[6] has had an interesting history from the time of its discovery up to the present day. It was "deliberately discovered" in 1869 at Vincennes, France by a French chemist, Mège-Mouriez. The invention was the result of a prize that was offered by Napoleon III in an attempt to procure a substitute for butter that would be cheaper than butter and less subject to rancidity. At that time, during the Fanco-Prussian War, butter was financially prohibitive for the poorer classes of people. Since 1869 the quality of margarine, its popularity, mode of manufacture, as well as legislative opposition to it,[7] have increased in direct proportion to one another, although at the present time much is being done to suppress and decrease legal opposition to this product, which is, in reality, equal to butter in nutritive value, only 35 to 50 per cent as expensive, and far superior in keeping qualities.

In current practice, vegetable oils have largely replaced animal fats and oils in margarine manufacture. This is partially due to the fact that some states restrict the use of fats of animal origin in the process. A mixture of cotton-seed oil and coconut oil is a commonly employed vegetable ingredient in many factories. Formerly chemists used a mixture of olein ($C_{17}H_{33}COOH$)[8] and so-called margarin in making this butter substitute and hence called the produce "oleomargarine." Later they learned that the "margarin" they were using, and what they had thought to be the glyceride of margaric acid, was merely a mixture of palmitin ($C_{15}H_{31}COOH$)[8] and stearin ($C_{17}H_{35}COOH$)[8]. Thus the term is actually a misnomer.

[6] A federal law enacted in 1886 required the product to be labeled and designated as "oleomargarine."

[7] A federal tax of ¼ cent per pound is levied on uncolored margarine, and ten cents per pound on the colored product.

[8] Obviously the glyceryl esters of these acids are meant.—Editor.

Margarine manufacture is a practical application of one phase of colloid chemistry. It consists of mixing a fat or oil with proper proportions of milk under carefully regulated conditions to produce a smooth emulsion. Needless to say, it should have the same general physical properties as butter and should taste as nearly like butter as possible. To attain the proper taste it is necessary to use a perfectly bland fat. For this reason, neutral lard and carefully refined vegetable oils are selected. To provide the butter-like taste, ripened (soured) milk is thoroughly churned with the fat. The milk is first pasteurized at a temperature of about 200°F. This is somewhat higher than ordinary pasteurizing temperatures since it is desired in this case to kill *all* bacteria whether harmful or not. Next small portions of the milk are treated with a lactic acid forming bacteria (*Bacterium lactis acidis Leichmann*). These small portions are allowed to stand with increasingly larger volumes of milk until the entire amount desired has the characteristic taste of buttermilk. During the churning process, which is conducted under carefully regulated temperatures, flavoring constituents are added. Margarine contains, on the average, 80 per cent fats, 17 per cent milk, and 3 per cent flavoring.

In very recent times—in fact, within a few short months—the mechanical processing of margarine has been reduced to a minimum of operations. Formerly the product was manufactured by several steps including mixing, two chilling operations, working, blending, and finally, printing. The latest process in effect combines the chilling, working, and blending operations into one, thereby minimizing handling as well as mechanical power.[9] There are two methods of chilling that have been in use for a number of years. The first of these, which is nearly obsolete, is cooling the emulsion directly by spraying it with cold water as it slides down a chute. The disadvantages of this process are that the cooling is hard to control and that much of the milk is washed out of the suspension. The other process that is still in popular

[9] It was my especial privilege to observe a complete new unit in operation; however, I am pledged to refrain from explaining the process in detail since this new development is jealously guarded by the owners.

use employs a "chill roll" comparable to that used in lard manufacture. The chill roll is a large revolving steel drum, interiorly refrigerated by use of liquid ammonia. The emulsion is discharged on to the roll in a thin layer where it solidifies and is scraped off by a large knife. The solid flaky material is collected and conveyed thence to the "working" tables where it is kneaded; eventually it reaches the blender which incorporates the flavoring material, principally salt. Printing, the margarine term for cutting into blocks and packaging, is the final process.

Chemical tests are frequently made from time to time in the manufacturing process to insure a perfectly uniform product. Titrations are performed for free fatty acid content and also as an indirect method of determining the percentage of sodium benzoate, which, incidentally, is present in small amounts as a preservative. The familiar volumetric analysis ($AgNO_3$) is used to approximate sodium chloride content. The Kreis test for rancidity is very important in proper analyses, as are also frequent bacteriological examinations. Thus chemistry is truly the guiding beacon in this industry, just as it is in practically every other manufacturing field of importance.

CHAPTER V

Soap

"Americans are the world's champion users of soap. If all the soap used by the people of the United States in one year were to be loaded on to box cars, at regulation load weights, the train would reach from Chicago to Pittsburgh, a distance of approximately 475 miles. What a lathering that much soap would make!" (10)

According to a popular legend, the Romans were the first actual soap manufacturers in the world; however, they stumbled on to the process quite by accident, and even then were not aware that their product was not a peculiar miracle of the gods. It was the custom of the early Romans to sacrifice slaughtered animals on Sapo Hill, a place of worship just outside of Rome. In time the rains had washed a considerable amount of melted tallow and greases from the animals, wood ashes from the fires, and soil down

to the banks of a small stream at the foot of the hill. The women of Rome soon became accustomed to doing their laundering in the dirt of the stream at the foot of Sapo Hill rather than any place else because the clothes seemed to clean most easily there. The explanation is, of course, that the K_2CO_3 of the wood ashes had united with the fats to produce soap in primarily the same way that it is made today. The Romans thought that some divine power had given their sacred hill the peculiar property of producing this cleansing soil, but their curious investigation later led them to discover the true reason for the phenomenon.

Soap-making in America's early days was, for the most part, a household operation, since manufactured soap was comparatively expensive. Housewives saved the fats and greases from cooking and the wood ashes collected from stoves and fireplaces, that accumulated throughout the winter. Each spring the amateur soap-makers would boil together in a large iron pot the fats and a liquor made from mixing water, straw, and lime with the wood ashes. The mixture was boiled without much regard for correct proportion or time limit and then allowed to cool to a semi-solid mass. The resulting soap was poured into containers, and the work of these "rule-of-thumb" chemists was over for another year.

Today soap-making has come to be a highly developed industry, largely through the work of two French chemists, Chevreul and LeBlanc:

"There were two men who may be regarded as the founders of the soap industry. One of these, Chevreul, was a trained chemist who did very remarkable work in the study of fats. . . . Chevreul went so far as to offer a theory of the hydrolysis of soap in water and his theory, although challenged by later investigators, is accepted today as correct.

. . . "The other man to whom the soap industry is vitally indebted is LeBlanc. . . . His profession was medicine but he also took great interest in chemistry.

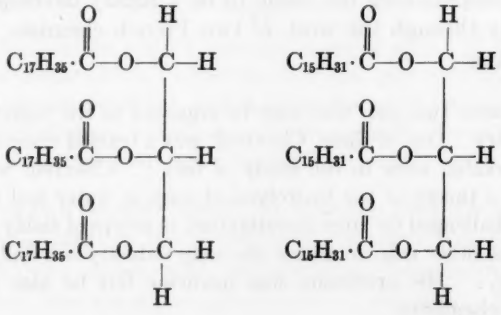
"Spurred on by the offer of a large money prize by the French Academy of Science, he developed, in 1790, a satisfactory method of obtaining sodium carbonate from common salt, and operated a factory for making soda for a few years." (14)

It is interesting to note that a few years later, an Englishman began to manufacture soda from sodium chloride, but had to give away tons of it to soap makers to overcome their prejudice and to assure them that his product was purer and more economical than the barilla[10] which they had been using.

Inasmuch as 85 per cent of the total inedible animal fats and oils are used in soap manufacture, the meat packing industry plays a large rôle in supplying this business with its raw materials. It might be mentioned, however, that in recent years soap manufacture and meat packing are growing farther apart in regard to the product which they have in common. This is due partly to the fact that packing house chemists are continually striving to convert all fats and oils into edible products, which, of course, command higher prices than inedible ones. Another factor is that vegetable oils are rapidly becoming more prevalent as raw materials in saponification.

There are two fundamental chemical reactions involved in saponification—namely, the hydrolysis of glycerides of fatty acids and glycerin, and the neutralization of the acids with an alkali to form soap and water.

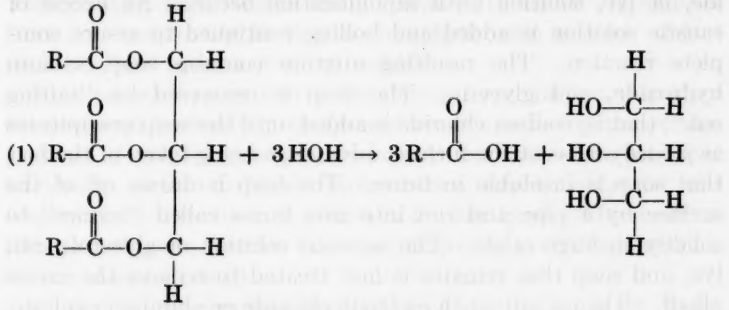
Stearic and palmitic glycerides are most commonly used and are represented structurally as follows:



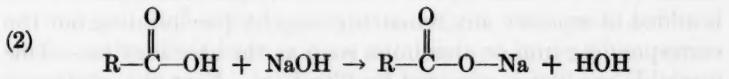
These are straight chain, saturated hydrocarbon derivatives occurring in varying mixed proportions with other fats and oils.

[10] Barilla is the ash from sea shore plants.

Since these fats are very resistant to separation, the quantitative determination of each constituent of the batch is still a very difficult problem to the chemist; however, the type reactions which take place are well understood and may be represented thus (R typifies an alkyl radical):



(1) $R{-}C(=O){-}O{-}CH(H){-}CH_2{-}O{-}C(=O){-}R + 3\,HOH \rightarrow 3\,R{-}C(=O){-}OH + HO{-}CH(H){-}CH_2{-}OH$



(2) $R{-}C(=O){-}OH + NaOH \rightarrow R{-}C(=O){-}O{-}Na + HOH$

To the beginning student in organic chemistry it may seem queer that the fatty acids between palmitic and stearic in the homologous series, namely, margaric acid ($C_{16}H_{33}COOH$), is not mentioned above. It so happens that members of this series containing an odd number of carbon atoms are very rare in nature; hence, margaric glyceride occurs only to slight extent, if at all, in animal fats, and is not worthy of consideration.

Technically speaking, a soap is a metallic salt of a fatty acid. However, contrary to popular opinion, very few soaps that are possible to make would be useful for detergent purposes. The reason for this can easily be seen with a little explanation. Sodium and potassium soaps are the only ones soluble in water; all others, such as calcium, aluminum, and magnesium soaps, are insoluble. These latter named soaps do have uses, however. Some of them function as impregnating agents in waterproofing oils, and some are used in varnish-making. Sodium soaps are hard, whereas those made from potassium hydroxide are soft.

The products of the methods of soap making in common prac-

tice include boiled soaps, cold-made soaps, hydrated and soft soaps, and high pressure soaps.

The process most widely used at present produces boiled soap. As might be indicated from the name, this is the product of boiling fat in a kettle or "soap pan" with a 10–20 per cent sodium hydroxide, or lye, solution until saponification occurs. An excess of caustic solution is added and boiling continued to assure complete reaction. The resulting mixture contains soap, sodium hydroxide, and glycerin. The soap is recovered by "salting out"; that is, sodium chloride is added until the soap precipitates as a curdy mass at the surface, advantage being taken of the fact that soap is insoluble in brine. The soap is drawn off of the surface by a pipe and run into iron boxes called "frames" to solidify in huge cakes. The aqueous solution of glycerol, salt, lye, and soap that remains is first treated to remove the excess alkali. Then a salt, such as ferric chloride or aluminum sulfate, is added to separate any remaining soap by precipitating out the corresponding iron or aluminum soap as the case may be. This insoluble product is removed by filtration. Next the solution is concentrated in a vacuum evaporator. At this stage of the process, salt is crystallized out and kept for repeated use. After the removal of the salt, the glycerin is further concentrated by evaporation until a nearly pure product is obtained. The successful operation of a soap plant depends to great measure upon the economical recovery of this important by-product. Glycerin is used chiefly in the manufacture of so-called "nitro-glycerin" and also automobile antifreezes.

Certain fats, mostly those of vegetable origin, possess the property of reacting with alkali at ordinary temperatures to produce soap. This operation, carried out in a machine called a "crutcher",[11] produces cold-made soap. Although heat is not usually necessary in this process, and a mild soap is the result of careful emulsion, nevertheless, the method is economically disadvantageous for several reasons: the glycerol remains in the

[11] In saponification jargon, stirring a soap is known as "crutching."

soap, it is difficult to make a neutral product, and more time and care are involved in "ripening".

Soft soaps, which occur as soft, jelly-like masses, are prepared in much the same manner as hard soaps, except that potassium hydroxide is used as the alkali instead of sodium hydroxide. This product also retains the glycerin. Hydrated soaps differ from soft soaps only in that sodium hydroxide is used, and of course a hard opaque product results.

High pressure soaps derive their name from the fact that they are prepared by heating the fat and caustic soda together under pressure of several atmospheres in an autoclave. The principal advantage is that a higher temperature may be obtained and consequently the time of reaction is shortened. Moreover, a sodium carbonate solution works satisfactorily at this temperature in lieu of caustic soda.

Evidently, the simplest method of saponification is by direct neutralization of a fatty acid by an alkali. Up until now the processes described have utilized the direct addition of the *glyceride* of the fatty acid to the alkali, which necessitates an intermediate chemical reaction as previously explained. In recent years a great boon to soap manufacturers has been the perfection of the Twitchell process for converting fats into the corresponding fatty acids prior to the actual soap making process itself. Oftentimes it is much more convenient to use the fatty acid in soap manufacture rather than the fat. For example, in lower grades of fats, such as garbage grease, so many impurities occur that it is not feasible to use the fat directly. Another advantage of the Twitchell process lies in the procuring of the glycerin before saponification without having to resort to as expensive a separation process as was mentioned heretofore. The Twitchell process is hydrolysis of a fat by means of a sulfo-fatty-aromatic acid as a catalyst, usually made by treating a solution of oleic acid in benzene with strong sulfuric acid.

Often in the advertisement of a popular brand of soap, one sees a statement as to percentage of purity. Purity, to the soap manufacturer, does not imply what it does to the majority of lay-

men; that is, purity, instead of referring to the quality of the ingredients, means the extent to which the soap has been neutralized. In other words, if a soap contains no free fatty acid and no free alkali, it is considered 100 per cent pure.

Floating soaps are made by beating air into the cooling product before it solidifies in order to reduce its specific gravity.

Soap, as it is placed on the market, whether it be toilet soap or laundry soap, usually contains a certain amount of filler, presumably to improve the efficiency, but really to cheapen the product. Many claims are made for the indispensable properties of these adulterants, but since soap itself is the best cleaning substance known, the value of fillers is greatly overstated. Common fillers used are borax, soda ash, talc, marble dust, starch, and others.

Part III. Miscellaneous By-products

CHAPTER VI

Fertilizers and Feeds

An industry that has been noticeably augmented as an outgrowth of meat packing is fertilizer and feed manufacture. Although this industry is not so dependent upon the packing house for maintenance as are others that have been described, still a great deal of fertilizer has packing house refuse as its source.

The value of fertilizer in plant growth has been known for a long time, but it was not until the latter half of the nineteenth century that its use became widespread in America. One of the contributing factors to this development was the waste material from the packing house. Until that time no special care was taken to see that waste products were economically utilized. Instead, packers were glad to give away their trimmings and refuse in order to get it hauled away. Later they made a charge for this material and encountered difficulty in disposing of it. For this reason, the meat packer took up the fertilizer business as a sideline. It was not until the World's Fair of 1893 that meat packers displayed fertilizer as a by-product of their industry.

Again in recent years fertilizer has declined in importance as a

sideline of the packing house for two principal reasons. In the first place, it is the natural desire of the producer to get the most possible financial returns from his products. As we have seen previously, edible products command much higher prices as a rule than do non-edible ones; hence, the more by-products the packer can place on the market as food, the better his profit. Thus, by modern scientific efficiency, he has been able to convert much material that used to be considered waste into food products of various sorts for both human and animal consumption. Secondly, the fertilizer industry does not depend on the packing plant as a chief source of raw material. On the contrary, fertilizer manufacturers resort to mineral deposits and synthetic processes for the majority of their ingredients. The discovery of rich phosphate beds in South Carolina, Florida, and Tennessee has helped to make American fertilizer manufacturers independent of organic sources.

Much research has been done recently on the function of fertilizers in the soil, and, as a result, progress in proper crop production has been rapid. Plants need chiefly carbon dioxide and nitrogen for growth. Since both these substances occur in the earth's atmosphere to the extent of about 1.6 million million tons and 4000 million million tons respectively, there is little danger of the supply's being exhausted. However, nitrogen is not available to plants in the free state except in small amounts so it is necessary to "fix" it by chemical means. The soil, which provides the rest of the elements necessary to plant growth has the average composition shown in the accompanying table (28). These elements generally exist in certain definite compounds, namely, carbohydrates, fats, and proteins. In forming sugars, starches, etc., the plant relies on photosynthesis, a natural process by means of which water and carbon dioxide are combined into higher substances.

A general equation corresponding to this change is

$$6H_2O + 6CO_2 + \text{light} \rightarrow \underset{\text{grape sugar}}{C_6H_{12}O_6} + 6O_2$$

It is a well known fact that when a soil produces crops for

several years without being replenished it becomes depleted in valuable compounds. When animals graze in a field and are taken to a slaughter house, they also carry away important constituents. The cycle can be completed, however, and the soil at least partially balanced, if a portion of the slaughtered animal is returned to the earth in the form of fertilizer.

Fertilizer raw materials from animals include bones, hoofs, horns, scraps, blood, tankage, and tankwater. Since many

VIII

Composition of the Earth's Crust

ELEMENT	PERCENTAGE	ELEMENT	PERCENTAGE
Oxygen	50.02	Magnesium	2.08
Silicon	25.80	Hydrogen	0.95
Aluminum	7.30	Chlorine	0.20
Iron	4.18	Carbon	0.18
Calcium	3.22	Sulfur	0.11
Sodium	2.36	Phosphorus	0.11
Potassium	2.28	Nitrogen	0.03

IX

Percentage Composition of Plant Organic Matter (28)

CLASS OF SUBSTANCE	CARBON	HYDROGEN	OXYGEN	NITROGEN	SULFUR
Carbohydrate	44.4	6.2	49.4	None	None
Fat	76–77	11.8–12.4	10–11.9	None	None
Protein	50–55	6.9–7.0	20.8–23.4	15.8–19.0	0.3–1.7

animal feeds also come from these products, they will be considered in this connection.

Although many of the softer bones are utilized for glue stock, better grades of hard bone are made into knife handles and similar products, and some bone is burned into charcoal for use as filtering agents, various kinds of composition filler, etc.; undesirable bone stock is boiled, dried, and ground up for the manufacture of feeds and fertilizers.

Dried animal blood serves as an excellent fertilizer. As a feed, it is called blood meal or blood flour; it has a high protein content,

and for this reason is used extensively as a mixer in hog and chicken feeds.

"Dried blood, as prepared for fertilizer, is a dark reddish meal or powder containing about 17 per cent of ammonia, equivalent to about 14 per cent of nitrogen. When applied to the soil it decomposes readily, releasing ammonia that is converted into nitrates by soil bacteria, which are later, in their turn, to be utilized by plants. The rapidity of the decomposition depends upon such factors as the character of the soil, temperature, etc. This product has a high fertilizer value." (16)

The manufacture of blood meal is relatively simple. The blood is coagulated in steam vats, dehydrated as much as possible by high power presses, and then dried until the moisture content is about five to ten per cent by weight. Finally it is ground into fine granules in a large mill.

Hoofs and horns that are not white enough to be made into buttons, are calcined and ground into fertilizer.

Tankage is a general term for the product resulting from cooking meat scraps, bones, intestines, deceased carcasses, and bits of other waste material under steam pressure for six to eight hours. The solid matter remaining is dried and ground into a meal. Tankage has a fairly high percentage of ammonia and calcium phosphate according to the grade of stock used. Tankage is used almost exclusively for feeds, but occasionally if it contains too much adulteration such as hair, hoofs, or horns, which are excluded from feeds by law, it is used for fertilizer. A good grade of tankage has an analysis of 60 per cent protein, 6 per cent fat, 2 per cent crude fiber, and 7–10 per cent bone phosphate.

After residual grease and oils are skimmed off the top of tankwater, it is evaporated to a viscous fluid called "liquid stick." This material is often mixed with tankage before the final drying and grinding process.

"Cracklings" is the name given to the resulting product when animal tissues are dry-rendered, or cooked in a fat-melter, pressed to remove fat, and finally ground. Cracklings are used as a base in many different kinds of feeds.

Manufacturers are required by law to print the percentage composition figures of fertilizers on the container. A law also requires that the ingredients must be soluble in water. In former years a fertilizer was just a fertilizer, and not too much regard was taken for purity or scientific mixture to conform to the need of a particular kind of soil. In recent times, however, fertilizer standardization has become a chemically controlled unit in the industry. A principal sales point of a well known company is

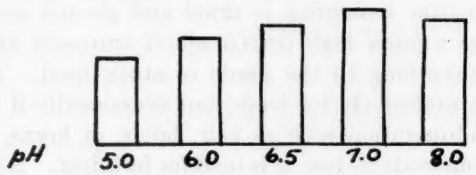
X

Percentage Composition of Some Feeds (16)

SUBSTANCE	PROTEIN	FAT	BONE PHOSPHATE OF LIME
Meat meal (tankage)	50–60	5–10	21.85 (maximum)
Meat scrap (cracklings)	50–60	5–10	21.85 (maximum)
Meat and bone meal or scrap	40–50	5–10	21.85 (maximum)
Blood meal	80–85	....	.....
Poultry bone (in various size)	20–25	3	40–50
Pure raw bone meal	20–25	3	40–50
Special feeding bone meal	5–10	....	65 (minimum)

XI

Effect of pH Value on Wheat



that their fertilizer is non-acid-forming. It has been found that plants in general grow best in a nearly neutral soil. Tables of pH values best suited for growth of certain crops are published by this company and instructions given for the amount of lime to use to correct acidities. This company also states that eleven elements including phosphorus, potassium, nitrogen, calcium, magnesium, sulfur, iron, boron, copper, manganese, and zinc are essential to proper plant growth, and gives rather conclusive evidence that the omission of any one of these elements results in

an inferior plant. Tests and improvements must be constantly carried out to meet the challenge of competition. Thus, efficient chemists are indispensable to a successful fertilizer works.

There are three main constituents by which the quality of a fertilizer is determined. These are ammonia, phosphoric acid, and potash. Fertilizers are usually designated by a series of three digits corresponding to the percentages of these substances present; for example, if the numbers 2–9–3 should appear on a fertilizer sack, it would indicate 2 per cent ammonia, 9 per cent phosphoric acid, and 3 per cent potash, or substances equivalent to these percentages. The packing industry furnishes only products containing nitrogen and phosphorus, however. In order to complete a standard fertilizer, other ingredients must be imported.

A product that cannot bear omission from a complete account of feeds, is dog food. To the layman, it may seem foolish to consider this product important, but in reality, this is one of the meat packer's pet products in all senses of the phrase. For dog food is not a conglomeration of meat scraps and anything else that can be swept from the floors, but is a scientific blend of meat, minerals, vegetables, and vitamins. Indeed, this product has been said to be the nearest approach to a concentrated food that has ever been successfully produced. If man ever takes his food in the form of pills, as some futuristic authors are wont to have us believe he will, he will probably be using a product that was a result of dog food experimentation.

That dog food has been a successful product is evident by the fact that it is the second most widely sold canned food in the United States. A large Chicago packing plant is now rearing the fourth generation of chow dogs in their research laboratory that have been fed on their dog food and water alone.

CHAPTER VII

Hides and Skins

Leather making concerns processes more of engineering control than it does typical chemical changes. Proper curing and tanning

of hides depends to great extent upon strength of solutions, their pH values, bacteria inhibiting power, etc.

The first step in hide curing is the application of dry salt to all surfaces of the skin soon after removal from the animal and preliminary cleansing. The hides are piled in the refrigerated hide cellar flesh side up, with about sixty pounds of salt for each one. They are left thus until needed. Sodium chloride, in solution of sufficient strength, will prevent bacterial growth almost in entirety. It is a fact that as the skin absorbs the salt, it also loses a large percentage of water.

At the beginning of the actual tanning operations, the skins are soaked in vats of water to remove salt and to restore the moisture lost in salting. The next procedure is called "fleshing," wherein the hide is scraped free of all adipose tissue clinging to the inner surface. Further washings follow fleshing. The skins are soaked for several days with a change of water daily.

The skins are then placed in a lime bath for two days to separate all hairs and glands from the skin proper. The bath consists of a saturated solution of $Ca(OH)_2$ with a small percentage of sodium sulfide.

After the lime bath the skins are subjected to a process of dehairing and scraping, called "scudding." Further washing with running water removes the excess of lime.

The next procedure is termed "bating." The skins are transferred to a vat which is equipped with paddles and is filled with a dilute solution of proteolytic (digestive) enzymes and a salt to neutralize the alkalinity resulting from the lime bath. The effect of the enzymes is to dissolve the elastin fibers and all remaining keratose from the hair. Bating changes the plump, resilient skin to renewed suppleness.

The actual tanning may be done in either of two ways. The method that is now becoming obsolete is to use a tanning solution consisting of tannins[12] obtained from trees such as oak, hemlock, chestnut, quebracho, and mangrove. Many other trees and barks also yield tannins. The chemical change that occurs when

[12] The terms tannins and tannic acids are used quite interchangeably. Their exact chemical structure is still unknown.

the collagen fibers of the skin react with the tanning solution is not definitely known; however, the leather assumes properties quite different from the original skin. The strength of the solution is weak at first and then is gradually strengthened daily for about ten days. At the end of this time the leather is fully tanned.

The other tanning method that has been in practice for about forty years first requires a pickling bath of sulfuric acid and sodium chloride for the bated skins. A basic chromium salt, usually $Cr(OH)SO_4$, is then applied to the hide. In somewhat the same way that the tannins act on the hide, the chromium combines with the collagen to form leather. Leather tanned in this way will not dissolve in boiling water, whereas collagen fiber will. This simple test is often employed to determine if the leather is completely tanned. If a sample does not curl up in five minutes in boiling water, it is deemed fully tanned.

Leather must be treated with a colloidal suspension of oil in water in order to keep it pliable and strong. The oil slowly diffuses through the leather, lubricating the fibers, whereas the water evaporates.

Finally the skins are dyed and "finished" by treating with a sizing material such as gelatin or casein. This process gives to the product the characteristic luster of a good quality leather.

CHAPTER VIII

Glue and Gelatin

Generally speaking, glues and gelatins are not distinctly separate products, but are chemically the same, differing only in degree of purity. Therefore, there is no definite dividing line which distinguishes a gelatin from a glue; however, when the product is edible, it is known as "gelatin"; when it is a high grade product, but not pure enough for food, the appellation is "technical gelatin"; and all lower grades are classified as "glues." Since there is this close relationship between these products chemically, they are considered together in this paper.

One of the common fallacies most difficult to overcome in the public mind is that gelatins are derived from hoofs and horns.

Even should the manufacturer attempt to use these materials as a source for his product, he would fail for the simple reason that he could obtain no soluble extract upon boiling them with water. Instead, gelatins are derivatives of hides, bones, connective tissue, and cartilage. These products have high collagen content.

Collagen is one of several proteins that occur in the raw materials in glue and gelatin manufacture. Others, that are more or less undesirable, incidentally, include mucoid, mucin, albumin-globulin, keratin, and elastin. Proteins are extremely complex compounds, whose definite chemical structures are still highly debatable. They are considered as combinations of alpha-amino acids, upon which their chemical properties are dependent. The average composition according to Lowy and Harrow (25) is carbon, 53 per cent; oxygen, 23 per cent; nitrogen, 16 per cent; hydrogen, 7 per cent; sulfur, 1 per cent. Also some proteins contain traces of iron, iodine, and phosphorus. Their physical properties are chiefly due to the fact that they form colloidal solutions, of which gelatin is a typical example.

Collagen is the most important protein that we must consider since it occurs to greater extent than the others and is most readily converted to gelatin. Its empirical formula is given as $C_{102}H_{149}O_{38}N_{31}$. When collagen is heated with water at a temperature of 70°–90°C., the molecule adds water to become $C_{102}H_{151}O_{39}N_{31}$ (gelatin).

Gelatins, as they occur in the colloidal state, are non-crystalline solids or semiliquids, having a characteristic translucency.

The actual mechanical process of manufacture of gelatin begins with washing the stock, whether it be hides, bone, or connective tissue. The washing is done in one of several ways, usually in a machine which operates much like a family washing machine.

Before bone is to be processed for gelatin, it must be treated to remove mineral matter. This is usually done with muriatic acid (commercial HCl). The reaction is as follows:

$$Ca_3(PO_4)_2 + 4HCl \rightarrow 2CaCl_2 + Ca(H_2PO_4)_2$$

The resulting salts are soluble in water. Ossein is the name given the material obtained after extracting the mineral from the bone.

After preliminary washing, the stock is submitted to a liming bath. The function of the lime is to swell the skins, dissolve albumins and mucins, and to loosen the hair and epidermis. The process of liming could be done with any alkali of the correct pH value, but calcium hydroxide is the most successful for this reason: When suspended in solution, lime produces exactly the correct hydroxyl ion concentration. As the OH ions are gradually used up, more lime goes into solution, maintaining a constant equilibrium. In the case of more soluble alkalis, this ingenious method obviously would not work.

A second washing is necessary after liming in order to neutralize and remove the excess alkali. To this end, the stock is usually placed in a very dilute HCl solution, or often in the case of inedible gelatins, in a sulfurous acid solution. Sulfuric acid is impracticable due to the insolubility of the resulting calcium salt.

The stock is now ready for "boiling." This process might better be called by some other name since the temperatures of the vats (usually 70°–90°C.) are below the boiling point of water. It is this process in which collagen is converted to gelatin. The solution is drawn off in four or five different extractions. The temperature is increased, and fresh water is added after each extraction. In the production of edible gelatins, the solution is carefully filtered to remove all insoluble matter. The liquor obtained is only about two to five per cent gelatin, which, except in the case of high grade gelatins, is too weak to congeal. Hence, evaporation is necessary. In order to preserve the composition of the gelatin solution, the evaporation is done in vacuum pans by means of steam heat.

The evaporated solution is run in a thin layer on to a long rubber conveyor which passes through a refrigerator room, where the material jells. The jelly is then stripped off and placed in a drying tunnel. New and economical methods of jelling and drying, that are now replacing former processes, are resulting in a higher grade product. Hide gelatin and bone gelatin are usually distinguished according to source in the sale of the product.

The processes for manufacture of glue and gelatin parallel each

other so closely that a separate description of each one is hardly feasible. Glue, however, does not entail the care and extreme cleanliness that is necessary in edible gelatin manufacture. For example, in making glue, bones are seldom treated to obtain ossein before the boiling process. Extractions from the boiling vats are made until the solution is too weak to save. Ordinarily, formaldehyde (HCHO) is added to glue as a preservative. Zinc oxide (ZnO) and zinc sulfate ($ZnSO_4$) are also used to prevent decomposition and to add opaqueness.

Determinations made on gelatin to standardize it are:

1. Moisture content
2. Jelly strength (by means of a gelometer)
3. Viscosity
4. pH value
5. Bacteria count
6. Ash content
7. Metallic impurities (Cu, Zn, As)
8. Foam ability (should be low)

Gelatin is used not only as food itself, but also in making ice cream, candy, and so on. Gelatin finds important use in photography for the coating on photographic films and plates which carry the silver salt emulsions. Capsules and other delicate containers are also made of gelatin. Glue is all-important in manufacture; in fact, some wag has said that glue holds the world together. Glue is used for sizing in the manufacture of textiles and papers. Barrel and cask production, match manufacture, sandpaper making—all depend upon glue as a necessary raw material. Most of the tests for quality that are made on gelatin are also used in grading glue, although impurities are not of chief concern in this case.

CHAPTER IX

Pharmaceuticals

One of the most modern and as yet undeveloped industries that have evolved from the packing house is the manufacture of pharmaceuticals, the medicinal compounds that have their origin

in animal glands. The enormous growth of this industry in recent years is essentially due to latest research in psychology and medicine in regard to the function of glands, and the effect of their secretions upon mental and physical behavior. Until about forty years ago, scientists had only primitive knowledge of the endocrine glands, and not until the last decade or so has glandular therapy been more than a "crack-brained scientist's fond hypothesis." Moreover, the subject of endocrinology is still in its infancy in comparison to the advolution we have reason to expect

XII

Percentage Yields of Glue from Certain Raw Materials (16)

STOCK	MOISTURE	GLUE	GREASE	TANKAGE
Ossein	10	70–80	....	5
Green-salted calf stock	30–40	16	2	9
Green-salted hide stock	30–40	18	3	10
Hide stock, dry	10	35	1	5–10
Hide split, green-limed	50–70	14	....	5
Green-limed sheepskin	60	7	7	5–10
Coney stock (rabbit skin)	10	50–55	....	20–25
Fleshings, green-limed	50–70	8–12	5–12	5–10
Fleshings, dry	15	20–25	5–25	10–20
Sinews, salted	35–50	22–24	2– 3	7– 8
Green bones	40–60	10–12	5–20	25–45
Dry bones	10	18–20	1	60–70
Horn piths, dry	10–12	23	....	65

in future years. The field at present is rich indeed for the biological chemist.

When treatment of nervous disorders first became prevalent, the only practical source of proper pharmaceuticals was at the packing house; since glandular secretions occur in such limited amounts, it was necessary to appeal to a place where slaughter of animals was done on production scale. Up until that time, animal glands were not considered worth salvaging and were not carefully utilized as they are today.

The chemical composition of glandular products for the most part is not clearly known. Hence, synthesis of many of these compounds is out of the question, at least until organic structure

can be rather definitely ascertained. Synthetic production of these hormones, independently of the packer, is evidently a thing of the contingent future, inasmuch as Wilson & Co. is at present enlarging their already highly successful pharmaceutical laboratory and factory in Chicago.

The limits of this paper will not allow an extensive description and history of each glandular product; however, some of the more important and better known products are worthy of mention and explanation.

Pepsin, a substance containing a proteolytic enzyme, is obtained from the lining of the stomach of the hog. It occurs in

XIII

Yields of Gland Products (28)

GLAND	NO. PER LB. (FRESH)	LB. FRESH PER LB. DRY	NO. PER LB. OF FINISHED PRODUCT
Pituitary	148	5	740
Pituitary (posterior)	148	70	10,360
Ovary (cow)	80	6	480
Ovary (hog)	144	6	864
Ovary (sheep)	600	6	3,600
Ovary (cow) (corpus luteum)	80	20	1,600
Parathyroid	600	6	3,600
Suprarenal	40	630	25,200

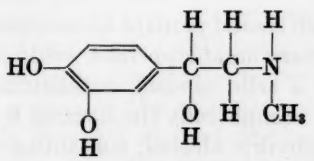
the human stomach and is necessary to the digestion of protein foods, such as meat, eggs, and cheese. According to the United States Pharmacopoeia standard, one part of pepsin dissolved in acidulated water will digest 3000 parts of egg albumin! This fact is rather startling, but when we read that by a new method of isoelectric precipitation, a purified concentrated form of pepsin has been produced whose proteolytic ratio is one to 70,000, we are even more awed. When extracted at the factory, pepsin occurs as a light yellow, flaky, crystalline solid, having no especially characteristic taste. An average dose for severe indigestion is one half gram of the substance in the presence of very dilute hydrochloric acid.

Rennin, diastase, lipase, and trypsin are other digestive en-

zymes of importance. The former is obtained from the lining of the fourth stomach of the calf. To give an idea of the strength of the standard compounds, one ounce of rennin will coagulate 186 gallons of milk in ten minutes. Diastase, lipase, and trypsin have their source in the hog pancreas; they are essential to digestion of starches, fats, and proteins.

"That the adrenal cortex is essential for life is now established beyond peradventure" reads an advertisement. This statement is quite true; the significant results of adrenalectomy are found to be loss in sodium chloride in the blood, increase in blood urea and potassium, decrease in muscular capacity, lowered resistance to infection, subnormal temperature, and poor appetite. Addison's disease is a direct result of improper functioning of this gland. Adrenal cortex extract, derived from cattle adrenal tissue, has proved to be invaluable in the treatment of the disease. Seventy-five grams of tissue are necessary to produce one cc. of the extract.

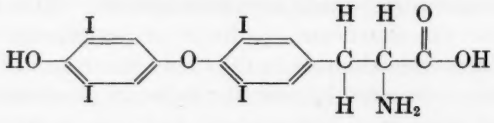
The inner portion of the adrenals, known as the medulla, has an entirely different function from the cortex. The cortex, yellowish-red in color, is derived from the mesoderm, whereas the reddish-brown medulla is of the same origin as the sympathetic ganglia. The medulla secretes epinephrine, a substance peculiar in that it is one of the few glandular extracts whose exact structural composition has been confirmed. Epinephrine is an odorless, crystalline, white or light brown solid, melting at 216°C. It oxidizes quite readily on exposure to air and for this reason is packed in tightly sealed brown bottles in an inert atmosphere. Its structural formula is:



Adrenaline, as this compound is unofficially called, causes increase in heart action, blood pressure, and glycogen in the blood. The

gland normally causes these conditions in the body when one experiences anger or fear.

Thyroxine, the chief hormone of the thyroid gland, is another compound that has been successfully synthesized (1927) by modern chemistry, and, consequently, is expected to replace the natural product from animal thyroid in time to come. It is a tyrosine derivative having the following structure:



Hypothyroidism slows the rate of basal metabolism, and is directly responsible for simple goiter, cretinism, and myxedema. The hyper condition (i.e., excessive thyroxine) causes excitability, nervousness, and increased metabolism.

In the treatment of diabetes a pharmaceutical called insulin has come to be indispensable for practicing physicians. Diabetes is a disease caused by deficient secretion of the "Islets of Langerhans" in the human pancreas, which control sugar content of the body and carbohydrate metabolism. When the sugar equilibrium is destroyed, sugar is literally spilled into the kidneys and appears in the urine. Drs. Banting and Best, two Canadian scientists, are noted for being the first to produce insulin (1921). Since that time Dr. John J. Abel of Johns Hopkins has succeeded in purifying the substance and has done valuable research in its use. Regulated injection of the compound results in nearly complete recovery from the malady, but, unfortunately, is not a permanent cure.

A compound which should perhaps be considered is cholesterol, which, as an elementary organic chemist would probably conclude from the name, is a solid alcohol, constituting a considerable portion of the bile. Empirically the formula is $C_{27}H_{45}OH$; structurally it is a monohydric alcohol, containing one double bond, and several condensed nuclei. Pernicious anemia is one of the diseases that has been successfully treated with liver extract; in fact, development has been so rapid that Clemen predicts results

as great in this line as those achieved with insulin in diabetes control.

Some of the more important glands and uses of their medical preparations are given in the following table (16):

In general when the glands are separated from the animal carcass, they are immediately chilled before trimming. Some of the glandular substances are quite unstable chemically at ordinary temperatures prior to preservative application; hence, great care

XIV

Glands and Uses of Medicinal Preparations Obtained from Them

Pituitary: Surgery, prevents shock; relieves gas pains. Obstetrics, contracts uterus, expels foetus
Pineal: Mental backwardness
Thymus: Rickets
Pepsin: Dyspepsia and digestive disorders
Rennin: Milk curdling for cheese making
Thyroid: Deficiency of the thyroid gland, simple goiter
Spleen: Supplies iron to the system
Orchic: Sexual neurasthenia
Suprarenal: Yields epinephrin, largely used in surgery
Suprarenalin: Powerful heart stimulant; increases blood pressure. Styptic, stops blood flow. Snake bites
Ovaries: Yields ovary extract and corpus luteum (part of the ovaries). Menstrual troubles; surgical and natural menopause
Mammary: Menstrual disorders
Pancreas: Yields insulin for diabetes treatment. Digesting foods, like milk, starch, and fat
Parotid: Replaces saliva in subject deficient
Parathyroid: Tetanus (caused by deficient parathyroid); paralysis agitans
Kephalin: Styptic, used in light surgery
Lecithin: Tonic
Thromboplastin: Treatment of hemorrhages; dental surgery
Red bone marrow: Tonic

is taken in early refrigeration. After being trimmed, the glands are packed and frozen into a solid mass to prevent spoiling during shipping. Upon arrival at the pharmaceutical plant they are carefully inspected, chopped up, and dried at temperatures low enough to prevent decomposition (about 130°F.). This drying is usually done in large ovens under a reduced pressure. The advantage in this pressure is to evaporate the water at a lower temperature than otherwise would be necessary. The next general

process is defatting by use of suitable organic solvents. Some more widely used solvents include alcohol (C_2H_5OH), petroleum ether (mixture of hydrocarbons within the gasoline distillation range), carbon tetrachloride (CCl_4), acetone (CH_3COCH_3), and ether ($C_2H_5OC_2H_5$).

After being defatted, the product is ground to a powder and sifted through a sixty or eighty mesh screen. Beyond the pulverized form, the different extracts may be put up in several

XV

Weights of Important Glands or Tissues of Meat-producing Animals (28)
(Weights in Grams, Ounces, or Pounds)

PORTION	BEEF ANIMAL	SHEEP	HOG
Pineal body	0.32 g.	0.04–0.12 g.	0.10 g.
Pituitary gland	3.0 g.	0.37–0.55 g.	0.33–0.78 g.
Ovary	5.7 g.	0.76 g.	3.15 g.
Testis	½ lb.	2 oz.	3–4 oz.
Suprarenal	11–15 g.	1.5–2 g.	3–5 g.
Thyroid	1–1½ oz.	2–9 g.	4–10 g.
Thymus	½–½ lb.	15–25 g.	9–35 g.
Pancreas	½–1 lb.	1 oz.	1½–2 oz.
Stomach	16–20 lb.	1–2 lb.	2–4 lb.
Spleen	1–2 lb.	¼–½ lb.	¼–¾ lb.
Kidney	½–1½ lb.	3–4 oz.	¼–½ lb.
Heart	3½–4½ lb.	½ lb.	½–¾ lb.
Lungs	4–5 lb.	½–1 lb.	1–1½ lb.
Brain and cord	20–26 oz.	6–9 oz.	10–16 oz.
Liver	10 lb.	1–2 lb.	2–4 lb.
Blood	30–40 lb.	3–5 lb.	5–10 lb.
Skin, vessels, etc.	65–75 lb.	12–14 lb.	Not removed
Bones and muscles	560–600 lb.	37–43 lb.	160–175 lb.

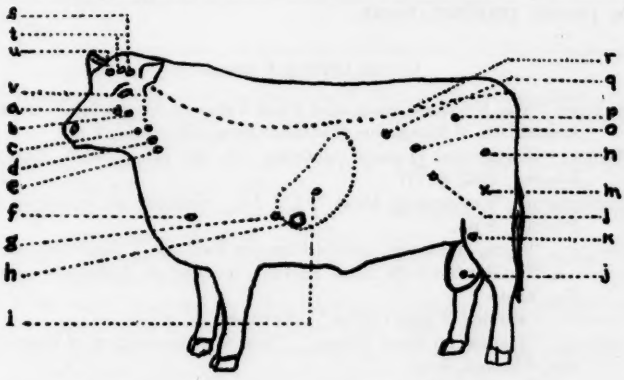
different forms, including liquids, tablets, capsules, and powder, according to the ultimate use for the product.

One of the largest problems the pharmaceutical chemist has to face is recovery of his solvents from the defatting process. One finds little reference in literature to the processes employed, but upon visiting a plant, he finds that a large part of the machinery is devoted to this very problem. Various methods involving

chemical and mechanical technique are employed. One method, filtration, is carried out by use of a Sweetland filter which uses diatomaceous earth to catch precipitates. The clear filtrate is drawn off at a spigot. In the recovery of alcohol, distillation is the principal method. At Wilson's pharmaceutical plant they

XVI

Sources of Medicinal Products from Cattle (16)



a. Tonsils
b. Paratoid
c. Submaxillary
d. Thyroid
e. Lymphatic
f. Red bone marrow
g. Liver
h. Gall
i. Pancreas
j. Testes (male)
k. Mammary (female)
l. Placenta (female)
m. Muscular tissue
n. Prostate (male)
o. Ovaries (female)
p. Colon (outer layer)
q. Suprarenal
r. Spinal cord
s. Pituitary
t. Brain
u. Pineal
v. Parathyroid

have a 24-column still extending the height of two stories which they use for alcohol recovery. Of course, the product obtainable is only about 95 per cent pure since alcohol forms an azeotropic mixture with water which cannot be further separated by fractional distillation methods. Rotators, operating on the gravi-

tational principles of the cream separator, provide still another method popular for solvent recovery.

It is a rather safe prophecy that pharmaceutical manufacture has a great future before it. In fact, so little is known of the chemistry of glandular products in comparison to what might be known, that ultramodern research is nearly certain to revolutionize the industry. It is estimated that the value of glands, pound for pound, in future will be many hundred times the value of the parent product, meat.

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CERTAIN NUCLEAR MASSES IN THE MACAQUE MEDULLA OBLONGATA

A Preliminary Report

FREDERICK DAVID GOUDIE

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CONTENTS

INTRODUCTION AND MATERIAL

This preliminary report of the configuration, position, and characteristic cell types of the cranial nerve nuclei and of certain other nuclear masses of the medulla oblongata of Macaca mulatta is intended as a basis for further consideration of the medullated and unmedullated fiber connections of these areas and as the morphologic background for the experimental studies now under way. Consequently particular stress is placed on the relative positions of these nuclear masses with respect to each other and to the surface of the brain, and their extents and variations in size at different levels have been established as accurately as possible, both by direct examination and by graphic reconstructions. Much less attention has been given to the finer cytological

structures of the individual neurons, largely because the material available at present is not adapted to such study, being cut at a thickness (50μ) which reveals in a more suitable manner the nuclear groupings.

This work is a part of the program for research on the primate nervous system being carried on by the Department of Anatomy of the University of Michigan. This project, as a whole, is made possible largely through grants from the Horace H. Rackham School of Graduate Studies of the University of Michigan, which is providing both material and technical assistance. The writer is very grateful for the opportunities opened to him by this grant. At this time he also wishes to express his appreciation to the Department of Anatomy of the University of Michigan for the privilege of studying the fine neurological material of Macaca mulatta prepared by the late G. Carl Huber, and especially to thank Dr. Elizabeth Crosby for the aid and inspiration which she has given to him during the time that this work has been in progress. Without her assistance and supervision this report would not have been possible.

The material which is available at present consists of transversely and sagittally cut serial sections of the brain of Macaca mulatta. These series have been fixed in the Huber trichloracetic solution and stained on the slide with toluidin blue.

CERTAIN PERTINENT LITERATURE

Details from accounts in the literature pertinent to the study of a particular nucleus are considered with the description of that gray mass and will not be given further consideration at this time. The writer wishes, however, to make brief mention of those reference texts and of contributions which are accounts of the macaque brain stem or that of closely related forms, that have been of particular value in interpreting the material. Among the reference texts is that of Ariëns Kappers, Huber, and Crosby (*5*), which has given the author a great deal of information from the comparative standpoint. The paper by Voris and Hoerr (*52*) on the medulla oblongata of the opossum has been very helpful in establishing likenesses and differences between a

lower mammal and the macaque. Aside from these, for each group certain reports were found to be very useful. In the study of the hypoglossal complex, the contributions of Vermeulen (*50*), Berkelbach van der Sprenkel (*9*), and Barnard (*7*) were consulted. The descriptions most used in the examination of the fasciculus solitarius and its associated gray were those by Freeman (*19*), DuBois (*15*), and Barnard (*6*). The publications of Weinberg (*56*), Castaldi (*14*), and Sheinen (*42*) were particularly suggestive in the work on the mesencephalic nucleus of the trigeminal, while that of Woodburne (*62*) was valuable in the study of the whole trigeminal complex. The experimental results of Ferraro and Barrera (*17, 18*) aided greatly the interpretation of the configuration of the dorsal funicular nuclei.

DESCRIPTION OF MATERIAL

The Hypoglossal Complex

The first cells of the hypoglossal nucleus appear at about the rostral end of the caudal half of the motor decussation (Fig. 3). At levels slightly behind its caudal tip a definite shifting dorsalward toward the central canal of the more dorsal cells of the ventral horn of the spinal cord can be observed. These neurons can be traced forward as a very indistinct, scattered cellular connection (of two or three cells) between the hypoglossal nucleus and the ventral horn neurons. The cells which make up this chain-like connection are typically motor in character (Fig. 3). This relation is in line with the observations of Barnard (*7*), who, in a preliminary report of his study of the hypoglossal complex in various submammals and mammals (including the opossum, the mouse, the dog, and man), found, in every instance, that the cells of the hypoglossal nucleus are more or less continuous with the ventral horn neurons of the spinal cord. It is also in accord with the earlier studies of Vermeulen (*50*) on Phocaena communis and Berkelbach van der Sprenkel (*9*) on the hedgehog, who noted similar connections between the ventral horn gray and the caudal end of the hypoglossal nucleus. Moreover, it agrees with the now generally accepted conclusion that the hypoglossal nucleus

is a forward differentiation, phylogenetically, of the ventral horn gray of the spinal cord (Ariëns Kappers, Huber, and Crosby, *5*). From this level of the motor decussation (Fig. 3) the hypoglossal nucleus of Macaca mulatta extends forward through the medulla oblongata to a plane cutting the open floor of the fourth ventricle, slightly caudal to the cephalic tip of the dorsal efferent nucleus.

The hypoglossal nucleus shows a grouping of its cells into a dorsomedial and a ventrolateral division (Fig. 4). The cells of the ventrolateral group, which make up the caudal pole of the nucleus, are linked by the few cells mentioned above with the ventral horn gray. The dorsomedial group appears first on the dorsomedial side of the ventrolateral group. Slightly rostrally, a few cells can be observed massing to form a lateral division (Fig. 4) of the nucleus, which lies lateral to the other nuclear divisions but persists for only a relatively short distance. The subdivisions of the hypoglossal nucleus have been studied by various observers. Among the contributions on this subject may be mentioned the work of Stuurman (*44*) on the mouse, that of Precechtel (*38*) on Elephas indicus (which he found to have a hypoglossal pattern similar to that of the mouse), the studies of the hypoglossal complex in various mammals by Vermeulen (*50*), who found the most primitive mammalian nucleus in Phocaena communis, and on the whale by Wilson (*57*), that of Berkelbach van der Sprenkel (*9*) on the hypoglossal complex of the European hedgehog, based on various embryonic stages, and especially the comprehensive study of Barnard, to be published shortly and as yet reported only in preliminary form, which contains descriptions of the hypoglossal complex in various submammals and mammals including the macaque.

As it is followed forward, a change in the position of the hypoglossal nucleus takes place. When the nucleus is first observed it lies lateral and slightly ventral to the central canal (Fig. 3), overlying the medial longitudinal fasciculus. Close above it are the cells of the dorsal efferent column, and, laterally, reticular gray. At the level of appearance of the dorsomedial group the nucleus retains its position ventral to the central canal. However, as this canal widens out into the fourth ventricle, the nu-

cleus underlies the trigonum hypoglossi but becomes separated from the ventricular floor by a small mass of lightly staining periventricular (Fig. 4, b) cells, which are continued forward into the nucleus paramedianus dorsalis. Soon this nucleus paramedianus dorsalis appears in the midline, medial and dorsomedial to the hypoglossal gray, which then is separated dorsolaterally from the vagal portion of the dorsal efferent nucleus by cells of the nucleus intercalatus (Fig. 5). The medial reticular nucleus lies ventrolateral to the hypoglossal nucleus, while ventrally there is reticular gray and a small group of cells, called Roller's nucleus in most texts (Winkler and Potter, *60, 61;* Ariëns Kappers, Huber, and Crosby, *5*; and others; see page 115; also Fig. 5). Medially the cells of the hypoglossal nucleus lie quite near the midline. The divisions of the nucleus change somewhat in their relative positions at different levels throughout the nuclear mass, but it is possible to distinguish dorsomedial and ventrolateral groups even at the cephalic pole of the nucleus (Fig. 5) although these groups appear to have merged before the rostral tip is reached. At this tip the hypoglossal is somewhat ventromedial to the dorsal efferent nucleus and ventral to the nucleus intercalatus.

The characteristic cells of the hypoglossal nucleus are of typically motor type (Figs. 3–5). In the caudal region of the nucleus they are somewhat elongated, with their long axes in the direction of the shifting chain of cells. As the nucleus becomes better developed its cells widen in the transverse plane, some becoming polygonal and others triangular in outline, and here they are more obviously multipolar. These neurons have a distinct oval nucleus with one or more evident nucleoli and show, in the toluidin blue preparations, numerous coarse Nissl granules. There are no evident differences in cell character in the three divisions of the hypoglossal nucleus of the macaque.

The grouping which is evident in the hypoglossal nucleus of mammals has led investigators to believe that a localization of motor function must exist within this cell group. In the brain of the hedgehog, Berkelbach van der Sprenkel (*9*) indicated that there is a functional pattern in the hypoglossal nucleus. He found a center for the geniohyoid muscle in the cephalic fifth of

the nucleus, distributing through the first hypoglossal rootlets, and a center for the hyoglossal muscle in the dorsal and for the styloglossal and the genioglossal muscles (the latter the more caudal) in the ventral part of the succeeding fifth of the nucleus. These last muscles are supplied through the medial and lateral rootlets, respectively, of the second hypoglossal root. In the middle fifth, the dorsal part has the centers for the longitudinal and the ventral part for the transverse muscles of the tongue. He located the centers for the ansa muscles—the thyroglossal, the sternohyoid, the sternothyroid, and the omohyoid—in the caudal two-fifths of the nucleus. This observer suggested that not all of the neurons of the hypoglossal nucleus are to be considered as somatic efferent, since the genioglossal may be said to be a branchiomeric derivative, and, in that case, its roots are to be considered as special visceral in type. An experimental study of the localization pattern in various mammals, including Macaca mulatta, is under way in the laboratory of the University of Michigan and will be reported shortly by Barnard. Consequently the matter need not be considered further in the present paper.

Before closing the account of the hypoglossal nucleus, brief consideration must be given to certain small nuclear masses which more or less encircle the hypoglossal gray. These are the nucleus intercalatus, the nucleus funiculi teretis, the nucleus praepositus, and Roller's nucleus.

The small celled, lightly stained nucleus intercalatus begins at planes through the rostral half of the hypoglossal nucleus (Fig. 5), and extends forward to the frontal pole of this nucleus, where it becomes continuous with the nucleus praepositus, although the line of demarcation between these cell masses is difficult to determine. At its caudal end the nucleus intercalatus lies beneath the floor of the fourth ventricle, between the dorsal efferent nucleus and the hypoglossal nucleus. In this position it forms, along with the hypoglossal nucleus, a prominence on the floor of the ventricle which is known as the trigonum hypoglossi. At a more rostral level the nucleus intercalatus appears to be made up of two parts, a dorsal portion lying directly above the dorsal

efferent nucleus and a more ventral group lying medial to that nucleus and dorsolateral to the hypoglossal nucleus. It is separated from the surrounding gray by fibers which swing ventral to the dorsal efferent nucleus and also by bundles which tend to pass dorsal to the hypoglossal nucleus. Slightly farther forward, the nucleus intercalatus enlarges somewhat on its medial surface and forms a cap over the hypoglossal nucleus. At the cephalic tip of the hypoglossal nucleus, the cells of the nucleus intercalatus are gradually replaced, beginning medially, by more deeply stained and slightly larger neurons, which are interpreted here as belonging to the nucleus praepositus (Jacobsohn, *26*). Various functions have been ascribed to the nucleus intercalatus. It is well established that it does not contribute to the hypoglossal roots (Berkelbach van der Sprenkel, *9*), but it has been regarded as a gustatory center by Ariëns Kappers (*4*), Fuse (*20*), and Berkelbach van der Sprenkel (*9*), as a vestibular center by Allen (*2*), who apparently included in it other more rostral gray, and as a proprioceptive center for tongue muscle and possibly pharyngeal and laryngeal muscles by DuBois (*15*). Recently Kimmel (*29*) described afferent fibers of the vagus to this region. Obviously cell preparations are not favorable for determining the functions of this nucleus and plans are under way for its study by experimental methods.

At levels where the nucleus intercalatus shows the two groups (p. 114), a tiny mass of small neurons, which stain slightly deeper than the surrounding gray, may be seen on the ventral side of the ventral group. They form a part of the encircling gray surrounding the hypoglossal.

The cell mass usually labeled as Roller's nucleus (Ramón y Cajal, *39*; Winkler and Potter, *60* and *61*; Ariëns Kappers, *5;* and others) is a fairly small, rounded nuclear mass situated ventral to the hypoglossal nucleus but distinct from it. This may not be the nucleus originally described by Roller (according to Crosby), but it is difficult to be certain from the account which he gave. It is possible that he had in mind a small-celled group such as that described by Schwentker (*41*) as consisting of autonomic neurons in man. If so, it has not been identified as yet

in our macaque material. The cell mass usually termed Roller's nucleus has multipolar neurons which resemble in general those of the reticular formation. Ramón y Cajal (*39*) was of the opinion that they were merely a frontal continuation of the reticular elements of the cervical cord. There is a difference of opinion as to whether or not this nucleus contributes fibers to the hypoglossal root (see Ariëns Kappers, Huber and Crosby, *5*).

The Dorsal Efferent Nucleus

In the monkey, the dorsal efferent nucleus first appears as a definite cell group at the level of the motor decussation (Fig. 1) and extends forward through the medulla oblongata to a plane just rostral to the cephalic extreme of the hypoglossal nucleus (Fig. 8A). This dorsal efferent nucleus gives rise to preganglionic fibers, and, slightly cephalic to its rostral tip, lie the inferior (Fig. 8A) and then the superior salivatory nuclei as the more frontal members of the same caudal general visceral efferent column. Just lateral to the caudal end of the dorsal efferent nucleus lies the accessory nucleus containing the cells of origin of the spinal accessory nerve, but between the two nuclei there appears to be no cell continuity such as Ariëns Kappers (Ariëns Kappers, Huber, and Crosby, *5*) described for the sheep. Dorsolateral to the dorsal efferent nucleus at this caudal extreme is the central canal and medial and dorsal to the nucleus are tiny scattered neurons of the nucleus of the commissura infima and its associated crossing fibers (Fig. 2), while ventrolaterally and ventrally, but well separated from it, are the larger motor neurons of the ventral horn. Although, at this caudal level, the cell bodies constituting the dorsal efferent nucleus are not numerous, they are so characteristically those of preganglionic neurons in size, shape, and type of Nissl granules that they are easily distinguished from the surrounding gray.

In this region of the nucleus, Vermeulen (*50*) described an interesting relation existing in Phocaena communis, which, according to Ariëns Kappers, Huber, and Crosby (*5*), is an excellent example of neurobiotactic influence. He found that the caudal ends of the nuclei are connected, right and left, by a com-

missural nucleus, which is less developed in these forms than in the giraffe and the camel. Such a connection is not present in Macaca mulatta.

As the dorsal efferent nucleus (Fig. 3) is followed forward in the series, ventral to it appears the hypoglossal nucleus, from which it is separated by a few scattered cells and from which it is clearly differentiated by the differences in cell type, the hypoglossal cells being typical somatic efferent neurons. Caudal to about this plane the neuraxes arising from the dorsal efferent neurons enter the bulbar accessory root while from approximately this region forward the neuraxes of these neurons enter the vagus root. This nucleus has been gradually enlarging caudorostrally and, slightly in front of this plane, an upward and medial extension of its cells forms a dorsomedial group and the remainder of them shift lateralward and increase in that direction to form a ventrolateral group (Fig. 4). In some regions these groups are relatively distinct but in others they tend to be interconnected by more scattered cells. They persist for some distance along the open floor of the ventricle but disappear as distinct groups before the rostral pole of the dorsal efferent nucleus is reached.

The dorsal efferent nucleus has attained a considerable size at the level of the calamus scriptorius (Fig. 4), although the area occupied by it is not so large as that covered by the hypoglossal nucleus, from which it is separated by a few scattered neurons that continue into the nucleus intercalatus. Laterally and dorsolaterally there lies the nuclear gray of the fasciculus solitarius. As the ventricle widens out the relations in the regions change somewhat; medial and ventromedial to the dorsal efferent nucleus is the hypoglossal nucleus, separated in part from it by the nucleus intercalatus. Ventrolateral, lateral, and dorsolateral to it is the gray surrounding the fasciculus solitarius, and ventrally is the medial reticular nucleus (Fig. 5). The dorsal efferent nucleus is separated from the floor of the ventricle dorsomedially by the lateral part of the nucleus intercalatus.

The proportionate amount of the dorsal efferent nucleus in front of the calamus scriptorius region as compared with the amount of this nucleus caudal to that region varies in different

mammals. In Macaca mulatta the larger part of the nucleus lies along the open floor of the ventricle, although there is a considerable stretch of nucleus in sections showing the central canal. In some mammals these conditions are reversed. Thus Vermeulen (*48*) reported that in no other mammal had he seen so large a part of the dorsal vagal nucleus lying at levels of the medulla cutting the central canal as in the giraffe (Camelopardalis girafa). According to this same observer, in the horse, the ox, and the sheep, two-fifths of the nucleus lies behind the calamus, in the pig and the dog the nucleus is nearly equally divided between levels of the medulla oblongata having the closed canal and those showing an open ventricle, and in the goat, the llama, and the camel three-fifths and, in the giraffe, no less than four-fifths of the nucleus are situated caudal to the calamus scriptorius.

The cells making up the dorsal efferent nucleus at its caudal end are large, lightly staining, multipolar neurons, showing the typical preganglionic shape, size, and type of Nissl granules. Such a neuron has a light staining nucleus, with a minute nucleolus. Occasional smaller cells are found intermingled with the larger neurons, more particularly along the borders of the nucleus and at its caudal and cephalic poles. As the nucleus enlarges, the number of typical preganglionic cells increases.

It is generally conceded that the dorsal efferent nucleus of primates is made up of the cells of origin of preganglionic fibers of which the more caudal become components of the bulbar accessory nerve and the more cephalic are components of the vagus nerve. Opinions differ as to whether or not a preganglionic center for the innervation of the heart is situated in the dorsal efferent nucleus or in the nucleus ambiguus. Malone (*35*) stated that, in man, the former nucleus has the cells of origin for the preganglionic fibers carrying inhibitory impulses to the heart by way of synapse in the cardiac ganglia, and identified a group of larger cells, intermediate in type and size between the remaining cells of the dorsal efferent nucleus and the hypoglossal nucleus, which he regarded as forming this cardiac center. Many other investigators (Molhant, *'35a*; Wainstein, *53*; von Husten, *25*) have tended to agree with Malone by placing the heart center

in the dorsal efferent column, but there is not unanimous agreement as to the localization pattern. For example, Kosaka (*31*) placed the heart center of the dog within the most ventral part of the distal third of the nucleus ambiguus. Ariëns Kappers, Huber, and Crosby (*5*) stated that it would be surprising if there should be a confirmation of this localization for the heart center in the nucleus ambiguus, since other preganglionic fibers of the vagus lie within the dorsal efferent nucleus. However, Crosby is of the opinion that, since the nucleus ambiguus and the dorsal efferent nucleus arise during the embryonic development of mammals from a common dorsally placed visceral efferent column, as Windle (*59*), Kimmel (*29*) and others have shown, the cells supplying preganglionics to the cardiac ganglia for the heart may, in some mammals, retain their more dorsal position and remain as components of the dorsal efferent nucleus and, in other mammals, migrate with the cell bodies of neurons supplying branchiomeric muscles to form the nucleus ambiguus.

The Inferior Salivatory Nucleus

The inferior salivatory nucleus is a small patch of preganglionic neurons directly rostral to the dorsal efferent nucleus (Fig. 8a), and slightly in front of the plane shown in figure 6. It lies medial to the gray of the fasciculus solitarius. This nuclear mass gives rise to preganglionic fibers of the glossopharyngeal nerve. A later detailed description of it is to be given in connection with a series of experiments which involves this nerve.

Gray Associated with the Fasciculus Solitarius

The gray associated with the fasciculus solitarius (Fig. 8B) forms a well developed nuclear group as far caudalward as the lower extreme of the motor decussation and, below that, grades over into the cell masses at the base of the dorsal horn of the cervical cord (Fig. 1). This statement is in agreement with that of Freeman (*19*), who found, on examining this bundle and its associated neurons from the standpoint of a column, that they occupy the portion of the medulla corresponding to the pars intermedia of the spinal cord, and therefore the neurons are a direct

continuation of that column into the brain stem. DuBois (*15*), studying the opossum, further substantiated Freeman's conclusions by pointing out that the tractus solitarius with its attendant nuclear gray holds a median position at its lowermost levels, being situated only a very short distance from the median raphé. Both of these investigators have discussed at some length this conception that the gray of the fasciculus solitarius is a direct continuation forward of the visceral column of the spinal cord.

At the region of transition from cord to brain stem, a well developed band of cells, associated with the commissura infima and known as the nucleus of this commissure, forms a midline connection between the gray of the fasciculus solitarius of one side and that of the other side of the brain (Fig. 1). The lower fibers of the fasciculus gracilis and the fasciculus cuneatus pass over the dorsal surface of the gray of the fasciculus solitarius and lateralward scattered neurons of this nuclear group form a cellular connection between it and the nucleus of the descending root of the trigeminal nerve. The caudal cells of the dorsal efferent column lie beneath the gray of the fasciculus solitarius, being separated from it by fibers, and the area ventrolateral to these cell masses is occupied by the decussating fibers of the pyramids.

As the series is followed forward the nucleus of the commissura infima becomes larger (*Fig. 2*) and the gray associated with the fasciculus lies dorsal to it. This gray touches dorsally on the scattered cells of the nucleus gracilis, and, after the appearance of the nucleus cuneatus, lies along the ventromedial surface of this last mentioned nucleus, and, as scattered cells, along its ventral border. Gradually the gray of the fasciculus solitarius, as it becomes wedged in (Fig. 3) between the nucleus gracilis and the dorsal efferent nucleus, takes on an irregular oval outline in cross sections and is demarked laterally by internal arcuate fibers. At certain levels there is a slight cellular connection between the nuclei of the two sides, which only prevails for a very short distance, but is quite definite where present. Then, as the calamus scriptorius is reached, the gray of the fasciculus solitarius, with the accompanying fasciculus, moves lateralward and the dorsal efferent nucleus tends to shift with it. The out-

line of the gray of the fasciculus solitarius changes somewhat as it migrates lateralward and it begins to assume the crescentic form which characterizes it rostrally, and which is very evident in figure 5.

In the mouse, at the level of the calamus scriptorius, Barnard (*6*) reported that the gray of the fasciculus solitarius and the fasciculus occupy a medial position above the dorsal efferent nucleus, while the ventromedial portion of the nucleus appears to be continuous with the nucleus intercalatus of Staderini. He described the nucleus intercalatus as being very small and not lying between the dorsal efferent nucleus and the hypoglossal nucleus, as is the case in the rabbit (Winkler and Potter, *60*). In the rabbit, as in the macaque, the nucleus of the fasciculus solitarius is somewhat lateral to these cell groups.

As the gray of the fasciculus solitarius assumes its crescentic shape (Fig. 5), it is concave laterally and convex medially, with the bundles of the fasciculus occupying the concavity. Ventrally, at this level, it is touched by scattered cells of the medial reticular nucleus; ventrolaterally, but separated from it by the reticular formation, is the nucleus of the descending root of the trigeminal; and, dorsolaterally, is the inferior vestibular nucleus. Medially and dorsomedially lies the dorsal efferent nucleus.

Beyond the rostral extreme of the dorsal efferent column, in the rostral third of the gray of the fasciculus solitarius, this gray loses its crescentic shape and becomes elongated, although it still maintains a concavity for the associated tract. It lies farther from the ventricle, with the inferior salivatory nucleus on its medial side (but just beyond the plane of the figure), and its other significant relations as shown in figure 6. It is quite evident that at this level there is a ventrolateral expansion of the gray of the fasciculus solitarius, the cells of this expansion tending to blend with those of the ventrolaterally lying nucleus of the descending root of the trigeminal. Certain cells (with intermingled smaller neurons) lying in relation to this ventrolateral expansion and medial to the nucleus of the descending root of the trigeminal constitute the nucleus parasolitarius (Fig. 6), which is recognized as being the receptive center for general visceral afferent im-

pulses. It has essentially the same relations as those characterizing it in other mammals (DuBois, *15*; and Barnard, *6*). This band of cells was first named the nucleus parasolitarius by Kohnstamm and Wolfstein (see Winkler and Potter, *60*).

The relationship between the gray of the fasciculus solitarius and the nucleus of the descending root of the trigeminal nerve is a matter of some interest. In planes through the nucleus parasolitarius (Fig. 6) the ventrolateral gray of the fasciculus solitarius actually blends with the nucleus of the descending root of the trigeminal, so that it becomes difficult to delimit sharply the two cell masses, a condition found also in other mammals such as the opossum (DuBois, *15*). At such levels the gray of the fasciculus solitarius is well developed, since it is receiving fibers from the glossopharyngeal nerve. Consequently the gray dorsal and medial to the fasciculus, sometimes spoken of as the dorsal visceral nucleus, is particularly enlarged, for the reception of gustatory fibers.

The gray of the fasciculus solitarius continues rostrally, in the macaque, in close relationship with the cells of the descending root of the trigeminal for some distance, but then tend to be separated from them by downsweeping fibers at some levels. When this occurs the nucleus is surrounded by nerve fibers on all sides. Dorsally, however, a few scattered cells of the medial vestibular nucleus are to be found on the nerve fibers and in relationship with the cells of the nucleus. Slightly above this level, cells of the descending root of the trigeminal arch over the fibers on its medial surface and lie ventrolateral to the rostral cells of the nucleus of the fasciculus solitarius. In this position the nucleus of the tract is somewhat smaller than it was at the level of the glossopharyngeal nerve, but it nevertheless still encircles the fasciculus. Beyond this level the fasciculus solitarius begins to break up and the cells of the nucleus continue on its dorsomedial side as a small group. This group enlarges and lies dorsomedial to the cells of the descending root of the trigeminal. Slightly in front of the level of entrance of the glossopharyngeal nerve the nucleus parasolitarius disappears and the remaining gray of the fasciculus solitarius diminishes greatly and soon becomes sepa-

rated from the nucleus of the descending root of the trigeminal. This gray of the fasciculus can be traced forward in the material to planes through the caudal end of the motor nucleus of the facial nerve. However, in the macaque the gray of the fasciculus solitarius, throughout the entrance of this nerve, does not show any marked enlargement such as has been seen at this level in the gray of the fasciculus solitarius in some other mammals, although not in man. In the primates, as has been seen, the evident enlargement dorsally occurs at the entrance of the glossopharyngeal nerve.

The small, lightly staining cells which make up the gray of the fasciculus solitarius are constant throughout, except for those of the nucleus parasolitarius, and are very similar to those constituting the nucleus of the descending root of the trigeminal. The neurons of the nucleus parasolitarius are larger and slightly more deeply stained.

Nucleus Ambiguus

Voris and Hoerr (*52*) described the caudal part of the special visceral efferent column of the opossum, an interrupted strand of cells in the ventrolateral part of the reticular formation of the medulla oblongata and the central part of the ventral horn gray of the spinal cord through the first four cervical segments. The spinal portion of this column, the accessory nucleus (Voris, *51a*), gives rise to the spinal accessory nerve; the medullar portion, the nucleus ambiguus, contains the cells of origin of motor fibers of the bulbar accessory, vagus, and glossopharyngeal nerves supplying striated branchiomeric muscle. Other observers, also, have described cellular continuity between the neuron group giving rise to the spinal accessory nerve and the nucleus ambiguus, but Vermeulen (*50*) believed such a relation to be purely secondary in character. Addens (*1*), of course, regarded these centers as quite distinct since he considered the spinal accessory to be a somatic efferent nerve. In any event, in Macaca mulatta these nuclear groups are separated.

The typical multipolar cells which make up the nucleus ambiguus first appear just rostral to the caudal end of the motor

decussation (Fig. 2). This level is somewhat behind the lower limit of the hypoglossal nucleus and slightly rostral to the beginning of the dorsal efferent nucleus (Fig. 8D). From its lower limit the nucleus ambiguus extends through the medulla oblongata (Figs. 2–6, 8D), varying greatly in size at different levels, to end at the caudal pole of the special visceral efferent nucleus of the facial nerve. Vermeulen (*50*) stated that the nucleus ambiguus in Phocaena communis passes sharply into the nucleus facialis, the special visceral efferent nucleus of the facial nerve. Various accounts in the literature indicate that its length varies in different mammals.

At its caudal extreme, where it is not very extensive, the cells of the nucleus ambiguus may be observed along the ventrolateral border of the bulbar gray, in close relationship with the tracts of the lateral funiculus (Figs. 2 and 3). Ventrally it is related to the lateral reticular nucleus and medially and dorsally to the scattered reticular gray. The dorsal cells of the reticular formation separate it from the cells of the descending root of the trigeminal nerve. These relationships are maintained in essentials throughout the extent of the nucleus ambiguus except that through the calamus scriptorius (Fig. 4) it shifts slightly dorsomedialward and then soon lies in the path of olivo-cerebellar and cerebello-olivary fibers among which some of its cells are scattered (Fig. 5). The relationship with the reticular formation is of particular interest. At certain levels there is a definite grouping of deeply staining reticular cells around the nucleus ambiguus, such as those which appear on its lateral border near its rostral pole (Fig. 6).

The nucleus ambiguus varies greatly in size and in distinctness at various levels, the number of constituent neurons varying from two or three to a dozen or more in a given field. At some levels the group is quite large and easily recognizable and at other levels it is very difficult to distinguish between the neurons of this nucleus and the cells of the surrounding reticular area. A variation from level to level is characteristic of this nucleus in mammals in general.

The cells at the caudal end of the nucleus ambiguus are typical

special visceral motor cells, since they are triangular in shape, somewhat elongated and larger than those of the dorsal efferent nucleus. They stain moderately and can be distinguished from the surrounding cellular areas. The cytology of these cells was studied with an oil immersion lens. They have a round to oval nucleus with a distinct nucleolus and the cytoplasm of the cell contains medium-sized Nissl granules, that is granules intermediate between those in the cells of the hypoglossal nucleus and of the dorsal efferent nucleus. At the level where the nucleus is made up of only a very few cells, these appear to be slightly larger than those at other levels and show a change in their general appearance. They are of the characteristic shape, but appear much clearer, with a more distinct nucleus and nucleolus.

The nucleus ambiguus gives rise, caudofrontally, to fibers of the bulbar accessory, the vagus, and the glossopharyngeal nerves which supply muscles of branchiomeric origin. It is planned during the coming year to make restricted lesions along the length of the nucleus ambiguus and also to cut selectively fibers of the various nerves arising from it in an attempt to establish a localization pattern.

Nucleus of the Descending Root of the Trigeminal Nerve

It is impossible in the macaque to observe differences between the cells making up the substantia gelatinosa Rolandi of the spinal cord and those constituting the nucleus of the descending root of the trigeminal, therefore one may say that the trigeminal nucleus found in the lower levels of the medulla oblongata is a continuation of the dorsal horn gray. At upper cord levels, to about the plane of entrance of the second cervical nerve, there is a thickening of the gray which marks the region of fusion between this gray and the nucleus of the descending root of the trigeminal, being an area of termination of both trigeminal and spinal cord fibers and thus of interrelation of pain and temperature impulses from the top and the back of the head and from the neck. The continuity of this spinal and medullar gray in the macaque is in line with the relations found in other mammals. Thus Freeman (*19*) stressed the direct continuation of the substantia gelatinosa

Rolandi and the nucleus of the descending root of the trigeminal and the likenesses between them in man, and similar relations have been described in the opossum (Voris and Hoerr, *52*), in the mouse (Woodburne, *62*), and in various other mammals. The nucleus of the descending root of the trigeminal (Fig. 8) is quite constant in size throughout its extent (figure 8C is a reconstruction of it within the medulla), but its shape and compactness are subject to change (Figs. 1 to 6). At the level of the motor decussation, caudal to the hypoglossal nucleus (Fig. 1), it is bounded medially by the fasciculus cuneatus. Ventral and ventrolateral to it is the dorsal spino-cerebellar tract and lateral to it the fibers of the descending trigeminal root, which at this level are from the ophthalmic division supplying the top of the head and the forehead.

Slightly rostral to this level (Fig. 2) the cells of the nucleus ambiguus take their position ventromedial and ventral to the nucleus of the descending root, being separated from this nucleus by scattered reticular cells. At this plane (Fig. 2) the characteristic cells of the main cuneate nucleus lie medial to the nucleus of the descending root of the trigeminal, while dorsolaterally are the fasciculus cuneatus and its overlying lateral cuneate nucleus. Soon, however, the cells of the lateral cuneate nucleus spread medialward (Fig. 4) over the nucleus of the descending root of the trigeminal, gradually displacing the fasciculus cuneatus, and, beginning ventrally, the chief cuneate nucleus, which disappears at slightly more rostral levels. Through these fields (Figs. 3 and 4) the lateral reticular nucleus, together with the longitudinal fiber bundles of the lateral field of the medulla oblongata, lies ventrolateral and ventral to the nucleus of the descending root while ventromedially is the nucleus ambiguus, medially the internal arcuate systems and intermingled reticular gray, dorsomedially the fasciculus solitarius and the neurons associated with it, and laterally the dorsal spino-cerebellar tract. In these planes the nucleus of the descending root of the trigeminal is crescent-shaped, with its concavity filled with lightly staining, island-like groups of cells, the more concentrated portions of the area lying laterally, ventrally, and dorsally. Slightly farther forward the

area becomes again more homogeneous in cellular arrangement and shows a dorsoventral elongation (Fig. 5).

These general relations remain much the same for many sections in following the series forward except that the lateral cuneate nucleus disappears and the vestibular gray then overlies the nucleus of the descending root dorsally and dorsomedially (Fig. 5). The intimate relation of this last mentioned nucleus with the gray of the fasciculus solitarius has been discussed earlier in the present paper (p. 121). Planes farther forward show the facial nucleus (Fig. 7) medial to the nucleus of the descending root of the trigeminal and separated from it by the emerging facial root. As the level of entrance of the trigeminal nerve is approached the nucleus of the descending root passes over into the chief sensory nucleus (Fig. 7).

In general the neurons constituting the nucleus of the descending root of the trigeminal in the macaque are small rounded to triangular elements, with fine Nissl granules. Occasional clumps of larger, multipolar neurons occur, which also show a fine Nissl granulation.

The work of numerous observers (Windle, *58;* Ariëns Kappers, Huber, and Crosby, *5;* and others; see also Crosby and Woodburne, in press) has indicated that the nucleus of the descending root of the trigeminal is the recipient of pain, temperature, and general tactile sensibility entering over the trigeminal nerve, with those impulses from the ophthalmic division distributing caudally and the maxillo-mandibular fibers reaching the more rostral parts of the nucleus. From this nucleus impulses are carried forward by the ventral secondary ascending tract of the trigeminal to the thalamus (Wallenberg, *54;* Woodburne, *62;* and many others).

The Chief Sensory Nucleus of the Trigeminal Nerve

This nucleus (Fig. 7) in the macaque is a rostral continuation of the nucleus of the descending root of the trigeminal nerve, a relation characteristic of many mammals (Voris and Hoerr, *52;* Ariëns Kappers, Huber, and Crosby, *5;* Woodburne, *62;* and many others). It is impossible to distinguish the level at which this transformation takes place by a change in cell type, since

both consist predominantly of small cells with occasional larger neurons (sometimes in small groups). However, the limits of the two nuclei can be determined approximately by certain anatomical relationships. As the rostral extreme of the nucleus of the descending root is reached in the series, the gray enlarges dorsally and frontally. This is well illustrated in the material, since in the series studied the sections through the chief sensory nucleus (Fig. 7) are distinctly oblique so that their upper portions are much farther caudal than their rostral portions. Consequently, the nucleus of the descending root is seen in the ventral part of the field, while above it and continuous with it is the chief sensory nucleus.

At its caudal extreme, the chief sensory nucleus covers a comparatively wide area, its dorsal limit being in line with the ventral half of the fourth ventricle (Fig. 7). Medial to this cell group, but separated by the fibers of the trigeminal nerve, lies the motor nucleus of the trigeminal, and dorsomedial are cells and fibers of the mesencephalic root of this nerve At various levels, strands of cells, intercalated between trigeminal root fibers, connect the chief sensory and the motor trigeminal nuclei. Toward its rostral end the chief sensory nucleus swings farther dorsomedially, and overlies the upper border of the motor trigeminal nucleus, after which it decreases rapidly and soon disappears.

This chief sensory nucleus is regarded as a tactile center (Windle, *58*), including probably two-point tactile sensibility. Various observers have traced ascending fibers forward to the ventral nucleus of the dorsal thalamus (Lewandowsky, *34;* Wallenberg, *54;* von Monakow, *36;* Le Gros Clark, *32*, *33;* Woodburne, *62;* and others).

The Nucleus of the Mesencephalic Root of the Trigeminal Nerve

An account of the nucleus of the mesencephalic root of the trigeminal in the monkey is to be found in Weinberg's paper (*56*). Consequently only certain facts concerning this nucleus and its root will be stressed here, particularly those which relate it to the locus coeruleus and the chief sensory nucleus of the trigeminal nerve.

The nucleus of the mesencephalic root of the trigeminal nerve, the caudalmost cells of which can be seen, in the macaque material, at a level just rostral to the caudal pole of the chief sensory nucleus of the trigeminal nerve (Fig. 7), extends through the upper pons region to end at the level of the rostral third of the oculomotor nucleus in the midbrain. This extent agrees, in general, with that found in other mammals. Thus Castaldi (*14*), in his studies on the guinea pig, reported that the main mass of this nucleus appears in sections through the rostral end of the oculomotor nucleus and its caudal pole terminates at the caudal end of the chief sensory nucleus of the trigeminal. Weinberg (*56*), in an extensive comparative study on the nucleus of the mesencephalic root, found a similar distribution of the cells in this nuclear mass in several mammals (including the macaque) and pointed out that, in general, the nucleus has a more caudal extent in higher mammals than in submammalian forms. According to van Valkenberg (*46*, *47*), the relations in marsupials, and especially in monotremes, show the sub-mammalian characteristics. Voris and Hoerr (*52*) found that in the opossum (Didelphis virginiana) the nucleus of the mesencephalic root begins at the level of entrance of the portio minor of the trigeminus root and is found at all levels anteriorly as far as the posterior commissure.

In the macaque, the cells at the caudal end of the nucleus of the mesencephalic root, although not numerous, are easily distinguishable, scattered in chain-like arrangement along the associated root somewhat dorsomedial to the chief sensory nucleus of the trigeminal and at the ventral extreme of the locus coeruleus, which separates them from the lateral wall of the fourth ventricle. Rostrally the cells of the nucleus become grouped along the lateral border of the locus coeruleus, these groups being made up of from two to four cells. Here the cell mass is better developed although it retains the same relationships as farther caudalward. As the number of cells of the nucleus increases, the group is separated from the lateral wall of the fourth ventricle by a thickened layer of the locus coeruleus. The nucleus of the mesencephalic root tends to follow the fibers of the root in a dorso-

ventral direction and the neurons constituting the locus coeruleus, which lie below the more ventral cells of the nucleus of the mesencephalic root, begin to extend laterally over the fibers of the root. As the locus coeruleus enlarges it lies dorsomedial to the upper tip of the motor nucleus of the trigeminal nerve, from which, however, it is well separated. The cells of the nucleus of the mesencephalic root do not follow this expansion, but increase dorsally and approach the lateral angle of the fourth ventricle, so that some lie dorsal and dorsolateral to the locus coeruleus. At about this same level the lateral expansion of the locus coeruleus tends to swing upward lateral to the fibers of the mesencephalic root. Rostrally the locus coeruleus is divided by the brachium conjunctivum into a ventrolateral and a dorsomedial division. Then, cells of the nucleus of the mesencephalic root can be seen along the lateral and dorsal borders of the dorsomedial group of the locus coeruleus, forming a cellular chain connecting with a group of cells of the nucleus of the mesencephalic root which lies at the angle of the fourth ventricle. Some cells of this type are scattered above the lateral angle of the ventricle and for many levels along the mesencephalic root, and still others farther forward in the lateral part of the anterior medullary velum. Such distribution within the anterior medullary velum is common to many forms (Voris and Hoerr, for opossum, *52;* Ariëns Kappers, Huber and Crosby, *5*). Rostral to this level the cells of the nucleus of the mesencephalic root tend to migrate dorsally, and are finally completely separated from the locus coeruleus. Beyond this level the nucleus passes dorsally and into the tectum, where it extends forward to near the frontal end of this region (see Weinberg, *56*).

The cells of the nucleus of the mesencephalic root are characteristically unipolar, sensory ganglion cells. They are large, round or oval in shape, with an oval nucleus, and have a deeply staining cytoplasm containing fine Nissl granules.

Observers in general (Weinberg, *56;* Sheinin, *42;* and many others), since the work of Johnston (*28*), have regarded the nucleus of the mesencephalic root as proprioceptive in function and as providing fibers of this type for the muscles supplied by the

oculomotor, trochlear, and trigeminal nerves, and perhaps other cranial nerves as well. The cellular type of the nucleus and the evidence obtained from a study of the fibers arising from its cells appear, in the writer's mind, to justify such a conclusion. However, certain excellent observers, among them Castaldi (*14*), still regard this nucleus as a motor center.

The Motor Nucleus of the Trigeminal Nerve

The motor nucleus of the trigeminal nerve appears caudally on the medial side of the caudal third of the chief sensory nucleus, separated from it by fibers of the trigeminal nerve (Fig. 7), and extends forward through the pons in this medial position for a comparatively short distance, terminating near the cephalic tip of the chief sensory nucleus. At first the motor nucleus, which is encapsulated by fibers on all sides except on the ventrolateral side where many scattered reticular cells can be seen, is small. However, it increases rapidly in size as it is followed rostrally, so that in its middle region it is nearly as large as the chief sensory nucleus. Through this middle region of the motor nucleus of the trigeminal nerve a small mass of gray made up of the same type neurons as those constituting the main portion of the nucleus (Fig. 7) can be seen on its medial aspect. Rostrally this small group enlarges dorsally and finally covers the medial side of the main motor nucleus and extends forward to the frontal pole of the nucleus, but throughout its extent it is separated from it, except for an occasional neuron.

The cells making up the motor nucleus of the trigeminal nerve are characteristic multipolar neurons, with deep staining cytoplasm, having Nissl granules similar to those of the nucleus ambiguus. The round to oval nuclei are relatively clear with prominent nucleoli. This nucleus, as is generally conceded, supplies motor fibers to the muscles of mastication.

The Dorsal Funicular Nuclei

The nuclei of this part of the medulla oblongata may be divided into three definite groups, the nucleus gracilis, the nucleus cuneatus, and the nucleus cuneatus lateralis.

The nucleus gracilis of the macaque appears as a few scattered cells among the fibers of the fasciculus gracilis at the uppermost end of the cervical cord (Fig. 1). It terminates at a level slightly cephalic to the calamus scriptorius. Judging from accounts in the literature (see Ariëns Kappers, Huber and Crosby, *5*), the size of the nucleus gracilis varies in different mammals. Thus it has only a limited extent in the opossum (Voris and Hoerr, *52*), is very small in cetaceans, which lack posterior extremities, but is more highly developed in ungulates and carnivores, where it may show lamination. In the macaque it is quite well developed but smaller than the nucleus cuneatus.

At the motor decussation the nucleus gracilis is made up of three parts, all lying within the dorsal funiculus medial to the posterior intermediate sulcus (Fig. 2). There is a midline group of cells close to the upper surface of the medulla oblongata and two lateral groups which extend, as a chain of scattered cells, about midway between the midline and a line drawn ventrally from the posterior intermediate sulcus to the central canal. The ventral cells of these lateral divisions fuse at the midline, thus giving the entire nucleus a "V" like appearance. Ariëns Kappers, Huber, and Crosby (*5*) referred to this midline nucleus as the nucleus of Bischoff (*10*). The cells of nucleus gracilis at this level lie intermingled with the fibers of the fasciculus gracilis on their lateral and medial sides in their upper and medial portion, while the ventral cells lie in relationship with the cells of the nucleus of the fasciculus solitarius laterally and with those of the commissura infima ventrally.

The nucleus gracilis tends to increase in size quite rapidly as it is followed forward. The medial group expands laterally to join a medial expansion of the lateral group. Then cells of the nucleus can be seen along the upper portion of the lateral group just beneath the surface of the medulla oblongata. At planes through the caudal end of the hypoglossal nucleus, the nucleus gracilis attains a comparatively large size (Fig. 3). Its cells are now arranged in columns lying in a ventrodorsal manner and occupying the greater part of the area from the midline to the posterior intermediate sulcus. This cellular arrangement gives the nucleus

a laminated appearance. Ferraro and Barrera (*17*, *18*) showed that, in the macaque, there is a pattern distribution of the fibers ending in the nucleus gracilis, in the sense that the fibers ascending in the fasciculus gracilis from the sacral and lumbar segments terminate in the more medial and more caudal portions of the nucleus, whereas the fibers ascending from the lower thoracic levels end in the more lateral and cephalic portions of the nucleus.

At levels near the calamus scriptorius, the nucleus gracilis, which has become a fairly compact and smaller cell mass, swings lateralward, lying near the surface of the medulla oblongata dorsal to the cuneate and dorsomedial to the lateral cuneate nucleus, and dorsolateral to the nucleus of the fasciculus solitarius. Its caudal tip extends forward for a short distance, dorsal and dorsomedial to the lateral cuneate nucleus, before disappearing.

In the macaque the cells of the nucleus gracilis are lightly staining neurons of the two types described by Ferraro and Barrera. One type is a medium sized cell, generally rather elongated and, at times, showing a slightly vesicular cytoplasm and excentric nucleus. The other type is a small neuron with finely granular cytoplasm and a rounded nucleus.

Nucleus cuneatus begins at a level slightly rostral to the caudal end of the nucleus gracilis (Fig. 2) and extends to a plane somewhat in front of the cephalic tip of the latter nucleus. The first neurons of the nucleus cuneatus form a tooth-like projection into its fasciculus from the dorsal side of the dorsal horn, slightly lateral to the caudal end of the gray of the fasciculus solitarius. Just in front of this level the nucleus of the descending root of the trigeminal nerve lies in close relationship laterally to the nucleus cuneatus (Figs. 2 and 3). Rostrally this latter nucleus enlarges and begins to shift dorsally along the medial side of the fasciculus cuneatus, displacing the fibers of this fasciculus. As this gray enlarges, it swings into a position close to the lateral portion of the nucleus gracilis medially, although still retaining its ventromedial relationship to the gray of the fasciculus solitarius. This nucleus shows a definite cell arrangement within itself, beginning as the open floor of the fourth ventricle is approached and continuing rostrally. At times this arrange-

ment takes the form of a concentric lamination, such as Ferraro and Barrera (*17, 18*) described, but the groupings may be according to other patterns, so that the pars rotunda and pars triangularis of the above observers can be identified. Such cell masses appear to the present writer to be the result chiefly of the intraarcuate fiber arrangement within the nucleus. In planes through the hypoglossal nucleus, behind the calamus scriptorius, there is no sharp line of demarcation dorsally between the nucleus gracilis and the nucleus cuneatus, and ventrolaterally and laterally the latter nucleus is in close relationship with the nucleus of the descending root of the trigeminal nerve. Ventromedially, however, the nucleus cuneatus is sharply separated from the dorsal efferent nucleus by the down-sweeping internal arcuate fibers originating from the nucleus gracilis. As the central canal widens out into the fourth ventricle, the nucleus cuneatus lies in the position indicated in figure 4. In these planes it is often interconnected with the lateral cuneate nucleus by cellular strands which extend between the fiber bundles, separating the two nuclear masses. The cells of the main cuneate mass, although small, are slightly larger than those making up the nucleus gracilis. Occasionally larger and more deeply staining cells are found on its lateral border, especially near the cephalic end of the nucleus. The lateral cuneate nucleus lies lateral to the chief cuneate nucleus. It appears rostral to the latter gray and extends cephalad to it. Its position, relative size, and relations are indicated in figures 3 to 5. It consists of cells which are larger and more deeply stained than those making up the main nucleus cuneatus.

As has been stated previously, the work of Ferraro and Barrera (*17, 18*) shows that a pattern arrangement exists within the nucleus gracilis and nucleus cuneatus based on a regional termination of the ascending fibers of the related fasciculi. Their results are in accord with the work of Bok (*11*) on the arrangement of the fibers in the fasciculus gracilis and the fasciculus cuneatus in man. It is evident, then, that the ascending proprioceptive and deep sensibility fibers constituting these tracts terminate in the nucleus gracilis and the nucleus cuneatus in such fashion that

those from the lower portions of the body end medially and caudally, and those from upper portions most laterally and, on the whole, farther forward, in a way approaching a segmental pattern, with the lateral cuneate nucleus receiving particularly fibers from the neck region. Through the nucleus gracilis and the nucleus cuneatus proprioceptive impulses are relayed to the thalamus by way of the medial lemniscus, the fibers of which show also a definite arrangement in course (Ferraro and Barrera, *17;* Crosby and Woodburne, in press) and in termination within the ventral nucleus of the dorsal thalamus.

The Reticular Gray

Throughout the bulbar portion of the brain stem of the macaque, as of other mammals, there are numerous large and small reticular elements, some of them arranged in groups and others appearing as scattered neurons among the fiber bundles or between other bulbar nuclei. At present only certain of the more prominent masses seen within the macaque medulla will be described, although a later, more detailed account is contemplated when a more complete knowledge of the fiber connections will give a further basis for an adequate subdivision of the nuclear masses.

In general all the reticular groups found at or near the level of entrance of the vago-accessory roots have been termed the nucleus reticularis inferior. Among such groups is a nucleus of the median raphé. The caudal part of this nucleus consists of a chain of cells at the level of the calamus scriptorius, on either side of the medulla near the midline, which extends from the medial angle of the hypoglossal nucleus downward to terminate at the dorsal border of the medial lemniscus (Fig. 4). Dorsally, slightly in front of this level, the cell chains constituting the nuclei of the two sides approach each other quite closely, but tend to spread apart ventrally, giving an inverted "Y" shape to the whole nuclear mass. As this nuclear mass passes rostrally it loses this appearance and rearranges itself as a band of cells along the midline. In more frontal sections (Fig. 6) scattered reticular cells lie on the fibers between it and the more deeply staining cells of

the more medial reticular gray and tend to establish a cellular connection between the two areas. The neurons constituting the caudal part of the nucleus of the median raphé (Fig. 4) vary in number, sometimes only a few being present while elsewhere they are relatively numerous. As the ventricle widens out, dorsal to the caudoventral part of the nucleus of the median raphé, a small, deeper staining, more closely packed group of neurons appears situated ventral to and in close approximation with the nucleus paramedianus dorsalis and continuous forward with the remainder of the nucleus of the median raphé. At about this plane a group of relatively large scattered reticular cells (Fig. 6) lies near the midline. This probably corresponds to the nucleus magnocellularis of Jacobsohn (*26*) but they do not fuse in the midline. They appear in planes through the lower part of the fourth ventricle and extend forward to a level caudal to the cephalic end of the nucleus ambiguus. They are illustrated in figures 5 and 6. Along the ventrally coursing hypoglossal roots and immediately lateral to them (Fig. 5) are scattered large and small reticular elements which correspond to the nucleus reticularis diffusus of von Kölliker (Ariëns Kappers, Huber, and Crosby, *5*). At some levels the other root fibers of the medulla oblongata show reticular groups along their course. The medially lying cells of this nucleus diffusus apparently constitute the nucleus funiculi anterioris of Obersteiner.

At some levels a concentration of the reticular elements lateral and then ventrolateral to the hypoglossal nucleus and root and lateral and then ventral, as the ventricle widens out, to the dorsal efferent nucleus constitutes a poorly delimited nucleus reticularis medialis but at other levels these grade over into the scattered reticular gray without nuclear subdivisions lying dorsal to the inferior olivary nucleus (Figs. 5–7).

At a level just rostral to the caudal tip of the nucleus ambiguus a fairly well delimited lateral reticular nucleus may be seen, which can be traced through the medulla oblongata to planes through the caudal portion of the lateral vestibular nucleus. Caudally, this lateral reticular nucleus (Fig. 3) is a minute, obliquely placed group of cells, ventromedial to the caudal

neurons of the nucleus ambiguus, indistinctly separated ventromedially and medially from the few remaining cells of the ventral horn and in such close relationship with fibers of the ventrolateral funiculus that it is sometimes called the nucleus funiculi lateralis. It increases quite rapidly in size ventromedially and ventrally, as it is followed rostrally in the series (Fig. 4), tending to assume an oval shape and to wedge itself beneath the nucleus ambiguus, but retaining its position internal to the paths of ascending and descending fibers through this field which represent the forward continuation of the ventrolateral funiculus of the spinal cord. This funiculus includes the ventral spino-cerebellar, the rubro-spinal, the lateral tecto-spinal, and the lateral spinothalamic tracts (joined here by fascicles of the ventral secondary ascending tract of the trigeminal). In relation with the lateral reticular nucleus are also fascicles of the lateral reticulo-spinal tract. In planes through the calamus scriptorius the nucleus shows a tendency to divide dorsoventrally into a dorsal group (d, ventral to the nucleus ambiguus), a medial group (m), and a ventral group (v), interconnected with each other and with the medial reticular gray by strands of more or less scattered reticular cells (Fig. 4). Slightly farther forward, the dorsal group diminishes considerably and the medial and ventral groups increase in size and then the groups become more or less fused.

At the same time a ventrolateral reticular group, which appeared slightly caudal to this level, spreads out over the entire lateral border of the inferior olivary nucleus, being intermingled with the olivo-cerebellar fibers (Fig. 5), and then thins out into a narrower band. Somewhat forward the various subdivisions of the lateral nucleus become continuous with each other to form a single gray mass which lies dorsolateral to the inferior olivary nucleus (Fig. 6). This mass is broken up into islands of reticular gray by the passage of fiber bundles and is connected by gray strands with the medial reticular nucleus and the nucleus reticularis diffusus. It extends from the region dorsal to the inferior olivary nucleus dorsolaterally around the ventrolateral border of the nucleus ambiguus. As the upper limits of the medulla oblongata are approached the lateral reticular nucleus is largely

lateral again, decreasing and disappearing except for scattered cells as the pons level is reached. This nucleus has medium sized to large multipolar neurons, apparently efferent in type.

A series of experiments to determine the connections and functional significance of the reticular gray in the macaque have been planned and are partly completed. These, which are being carried on in the Department of Anatomy, University of Michigan, in collaboration with Dr. Carl List of the Department of Surgery and Physical Therapy of the University Hospital, will be reported shortly.

The Inferior Olivary Complex

The inferior olivary complex in the macaque (Figs. 4–6) extends from planes through the caudal third of the hypoglossal nucleus to the level of the caudal end of the facial nucleus. It consists of medial and dorsal accessory olivary nuclei and a chief inferior olivary nucleus. The caudal tip of the medial accessory olivary nucleus appears just lateral to the pyramid and ventromedial to the lateral reticular nucleus, in line with the intermedio-lateral sulcus and along the ventrally coursing fibers of the hypoglossal nerve. A very short distance rostralward, a second, more ventral portion of this medial nucleus can be seen, lying slightly ventral to the first nuclear group (Fig. 4). These two groups unite almost immediately, and then very soon another discontinuous mass of this nucleus appears, dorsal to the preceding group, which also joins the others secondarily to form the medial accessory olivary nucleus. At about the same plane a fourth mass (Fig. 5) is seen which belongs with the medial accessory olivary nucleus but is united to its other portions only by scattered cells. The apparent discontinuity of this medial accessory nucleus is due to the marked convolutions which characterize it in the macaque.

The dorsal accessory olivary nucleus arises more rostrally than the medial accessory as a laterally placed cell group situated in planes where the medial accessory nucleus consists of three discontinuous masses. A second portion of this dorsal nucleus soon shows in the field (Fig. 5) and then the two parts join to form a single elongated cell band. For some distance, as the series is

followed forward, the dorsal accessory olivary nucleus remains much the same but then enlarges dorsomedially toward the dorsal, more or less independent tip of the medial accessory olivary nucleus, with which it is connected by a very few scattered neurons. This dorsomedial tip soon disappears and the medial accessory olive, due to folding, exhibits two subdivisions of which only the ventral persists. In the meanwhile the chief inferior olivary nucleus has appeared and the remainder of the medial accessory olive extends forward ventromedial to this chief nucleus as a club shaped mass with the thickened end of the club dorsomedial.

The chief inferior olivary nucleus, which in its middle portions is convoluted and U-shaped, is seen caudally at planes through about the middle portions (caudorostrally) of the medial and dorsal accessory nuclei, dorsolateral to the former and ventral and ventromedial to the latter nuclear mass (seen in planes just cephalic to figure 5). At such caudal planes the inferior olivary nucleus consists of first a single mass and then two distinct cell groups, a dorsal and a ventral, each composed of scattered neurons. Followed forward, both groups increase rapidly in size in a ventrodorsal direction. Soon they become continuous with each other to form the dorsal limb of the nucleus and then the nucleus expands dorsomedially between the dorsal and medial accessory olivary nuclei. At the same time the ventral part of the inferior olivary nucleus itself is enlarged and approaches the ventrolateral surface of the medulla oblongata, from which it is separated by the fiber bundles of the thalamo- (or strio-) olivary and ventral superficial arcuate systems. The inferior olivary nucleus now begins to assume its characteristic U-shaped form with the appearance of a ventral limb. The opening of the U points dorsomedially, so that a hilus is formed (Fig. 6).

For some distance rostrally, the relationships between the three components of the inferior olivary complex remain much the same, except that the ventral limb of the chief nucleus increases by adding another band of cells medialward. Then the dorsal and medial accessory nuclei begin to enlarge at their ventral and dorsal tips respectively, and the dorsal enlargement extends into

the hilus of the inferior olivary nucleus. In planes through the rostral third of the nucleus ambiguus, the medial cells of the dorsal accessory olivary nucleus tend to cap over the dorsolateral limb of the inferior olivary nucleus and then the dorsal nucleus shortens laterally and is reduced to a small cell group in the hilus of the inferior olivary nucleus. The medial accessory nucleus, which is separated here by a small clump of cells from the medial limb of the inferior olivary nucleus, also becomes smaller. As the upper limit of the medulla oblongata is approached, the accessory olivary nuclei both disappear but the inferior olivary nucleus itself continues forward to planes through the caudal pole of the facial nucleus.

In the toluidin blue material of the macaque medulla oblongata, the characteristic cells of the inferior olivary complex show somewhat round, small, deeply staining cell bodies. These elements give to this complex a highly distinctive appearance.

There are innumerable figures in the literature showing the inferior olivary complex in various forms and many studies of this gray have been made in various mammals. Its ontogenetic development in man has been considered by His (*21*), Essick (*16*), Streeter (*43*), and Kooy (*30*). It has been described and, in some cases, modeled for various primates by a series of observers, among whom may be mentioned Tilney (*45;* who found the inferior olivary nucleus relatively less well developed in Tarsius than in any other primate excepting the marmoset), Sabin (*40*) Weed (*55*), Jenkins (*27*), and Kooy (*30*). Various accounts of its connections have been given by Brouwer and Coenen (*12*), Kooy (*30*), Tilney (*45*), Wilson (*59*), and others. A summary of the phylogenetic and ontogenetic development and connections of the inferior olivary complex is available in the Ariëns Kappers, Huber, and Crosby text (*5*).

CONCLUSION

The foregoing account of the nuclear masses in the macaque medulla oblongata shows that the pattern in this primate resembles that seen in other mammals and is very like that in man except for differences in size of certain of the nuclear masses, for

example that of the inferior olivary complex. Since this paper reports anatomic relations which are being used as the basis of experimental work, no further summary will be given at this time.

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ABBREVIATIONS FOR FIGURES

ant.m.v., anterior medullary velum
b, periventricular gray
br.p., brachium pontis
com.inf., commissura infima
d, dorsal group of the lateral reticular nucleus
d.sp.cere., dorsal spino-cerebellar tract
dec.pyr., decussation of pyramids
des.root V, descending root of trigeminal nerve
dor.m.div., dorsomedial division of hypoglossal nucleus
fas.cun., fasciculus cuneatus
fas.gr., fasciculus gracilis
fas.sol., fasciculus solitarius
inf.cer.ped., inferior cerebellar peduncle
l.c., locus coeruleus
l.f., forward continuation of lateral funiculus of spinal cord
lat.div., lateral division of the hypoglossal nucleus
m, medial division of lateral reticular nucleus
m.teg.pr., motor tegmento-peduncular nucleus (Jacobsohn)
med.long.fas., medial longitudinal fasciculus
n.ambig., nucleus ambiguus
n.c.sup., nucleus centralis superior
n.com.inf., nucleus of commissura infima
n.cun., nucleus of fasciculus cuneatus
n.des.root V, nucleus of the descending root of the trigeminal nerve
n.dor.eff., dorsal efferent nucleus
n.dor.oliv., dorsal accessory olivary nucleus
n.fas.sol., gray of fasciculus solitarius
n.gr., nucleus of fasciculus gracilis
n.hyp., motor nucleus of the hypoglossal nerve
n.inf.oliv., chief inferior olivary nucleus
n.inf.sal., inferior salivatory nucleus
n.inf.vest., inferior vestibular nucleus
n.inter., nucleus intercalatus
n.l.cun., lateral cuneate nucleus
n.l.ret., lateral reticular nucleus
n.m.oliv., medial accessory olivary nucleus
n.m.ret., medial reticular nucleus
n.m.root V, nucleus of mesencephalic root of trigeminal nerve
n.m.vest., medial vestibular nucleus
n.mg.J., nucleus magnocellularis of reticular formation (Jacobsohn)
n.mo.V, motor nucleus of the trigeminal nerve
n.mo.VI, motor nucleus of the abducens nerve
n.mo.VII, motor nucleus of the facial nerve
n.para.sol., nucleus parasolitarius
n.para.dor., nucleus paramedianus dorsalis
n.prae., nucleus praepositus
n.raphé, nucleus of the median raphé
n. of Rol., Roller's nucleus (label should extend to immediately overlying group of cells in Fig. 5).
n.s.oliv., superior olivary nucleus
n.sens.V, chief sensory nucleus of the trigeminal nerve
N.V, trigeminal nerve
N.VII, facial nerve
N.VIII, auditory nerve
N.XII, hypoglossal nerve
p.gr., pontine gray
pyr., pyramid
ret.gr., reticular formation
s.cer.p., superior cerebellar peduncle
tr.gr., trapezoid gray
v., ventral group of the lateral reticular nucleus
v.IV, fourth ventricle
v.h., ventral horn of the spinal cord
v.h.n., ventral horn neurons
v.l., ventrolateral group of the lateral reticular nucleus
v.lat.div., ventrolateral division of the hypoglossal nucleus
v.sp.cere., ventral spino-cerebellar tract
Y, scattered cells from ventral horn gray toward caudal pole of hypoglossal nucleus

FIGS. 1 AND 2. Drawings of toluidin blue preparations of the macaque brain cut in a somewhat oblique plane, so that the more ventral part of each figure is slightly farther forward than the dorsal portion. Fig. 1 at the level of transition between the spinal cord and the medulla oblongata, through the caudal pole of the dorsal efferent nucleus, the commissura infima, and the nucleus of the descending root of the trigeminal. × 14.8. Fig. 2 rostral to figure 1, through the caudal tip of the nucleus ambiguus. × 14.8.

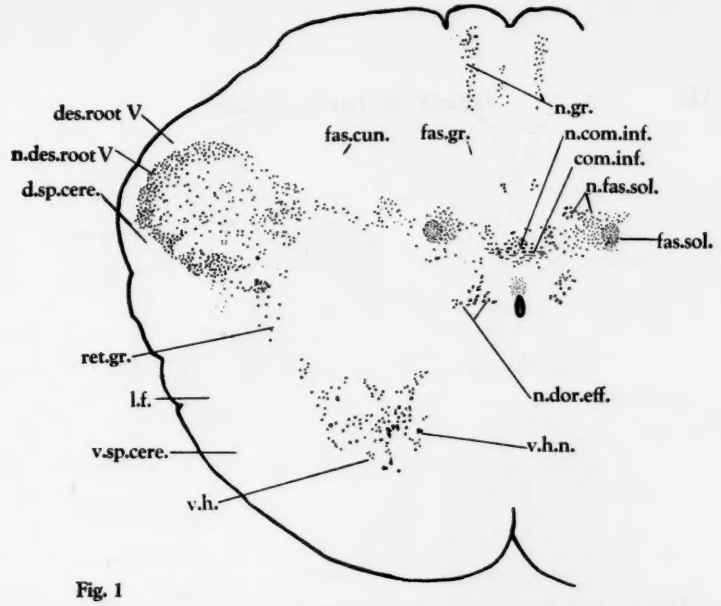
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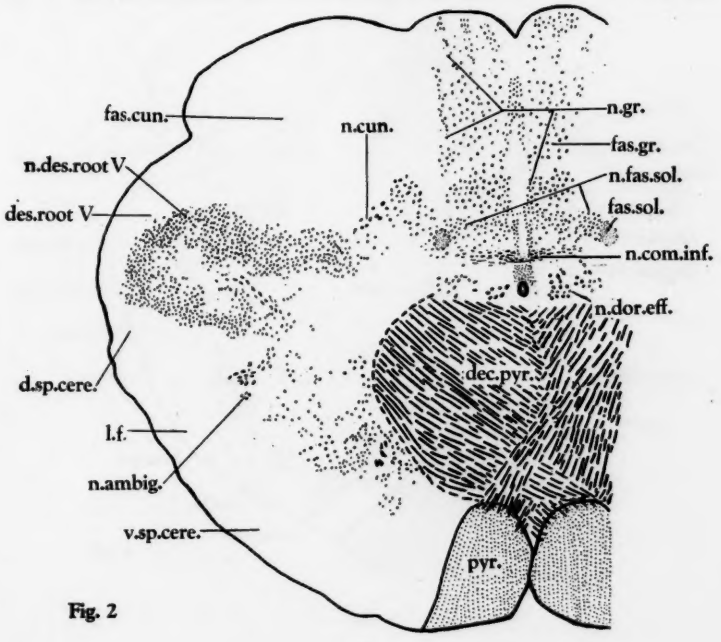
Fig. 1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fas.sol.
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dec.pyr.
pyr.

Fig. 2

FIGS. 3 AND 4. Drawings of sections from the same series as those illustrated in figures 1 and 2, but farther forward. Fig. 3 the relations of the fasciculus solitarius to the nuclei of the posterior funiculus and the dorsal efferent nucleus. × 12.9. Fig. 4 from a section rostral to that seen in figure 3, through the calamus scriptorius. The hypoglossal nucleus and the lateral reticular nucleus show typical subdivisions at this level, and the caudal tip of the medial accessory olive appears as two discontinuous cell masses in the ventral portion of the field. × 12.5

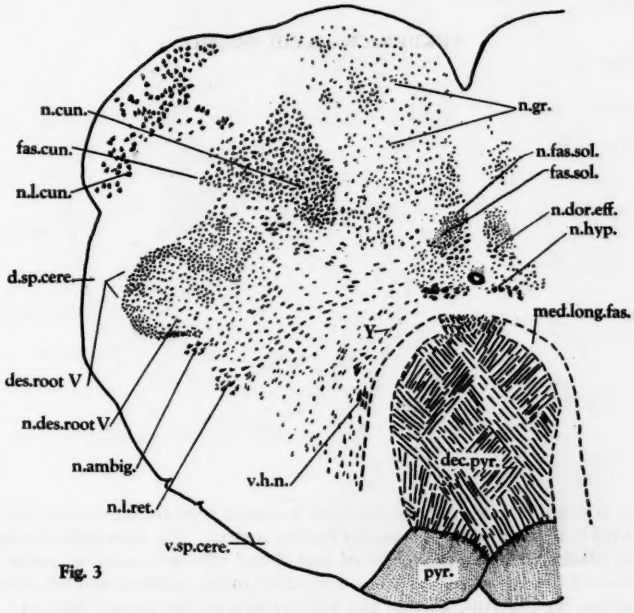
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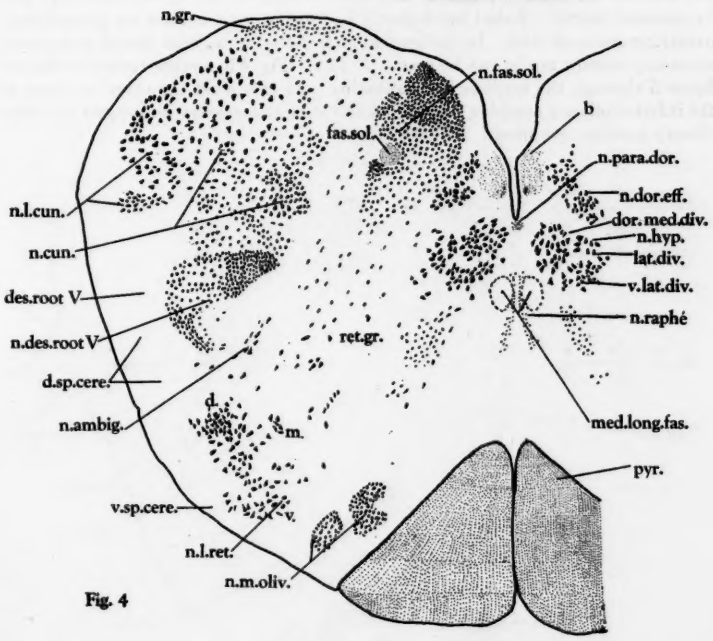
Fig. 3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pyr.

Fig. 4

FIGS. 5 AND 6. Drawings from the same macaque toluidin blue series as those illustrated in the preceding figures, but farther rostral. Fig. 5 medulla oblongata through planes where the hypoglossal and dorsal efferent nuclei lie under the open floor of the ventricle. Attention is called to the position and relations of the nucleus intercalatus, and to the subdivisions of the lateral reticular and hypoglossal nuclei. Label for Roller's nucleus should extend to immediately overlying group of cells. In the ventral part of the figure, both dorsal and medial accessory olivary nuclei can be seen. × 12.1. Fig. 6 in a plane rostral to that of figure 5 through the nucleus parasolitarius. At this level the three portions of the inferior olivary complex, the dorsal and medial accessory nuclei and the chief olivary nucleus, are shown. × 10.8.

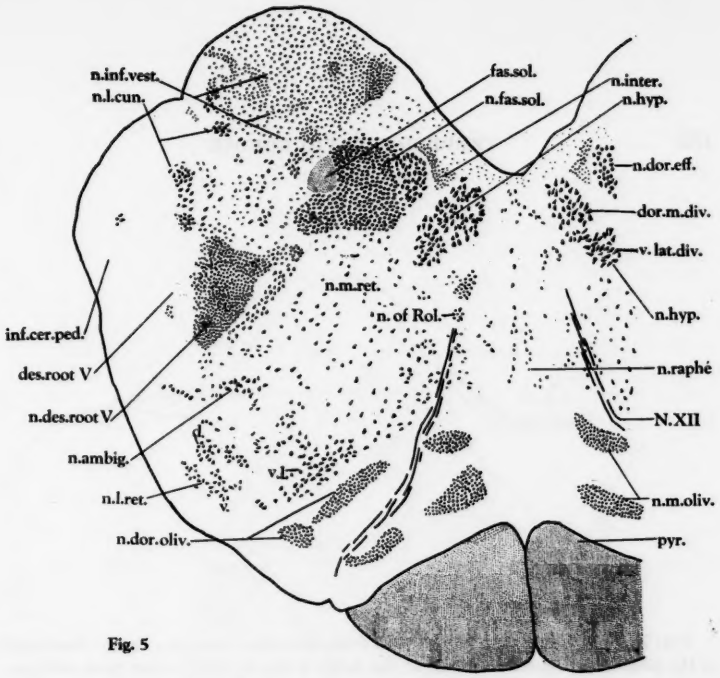
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Fig. 5

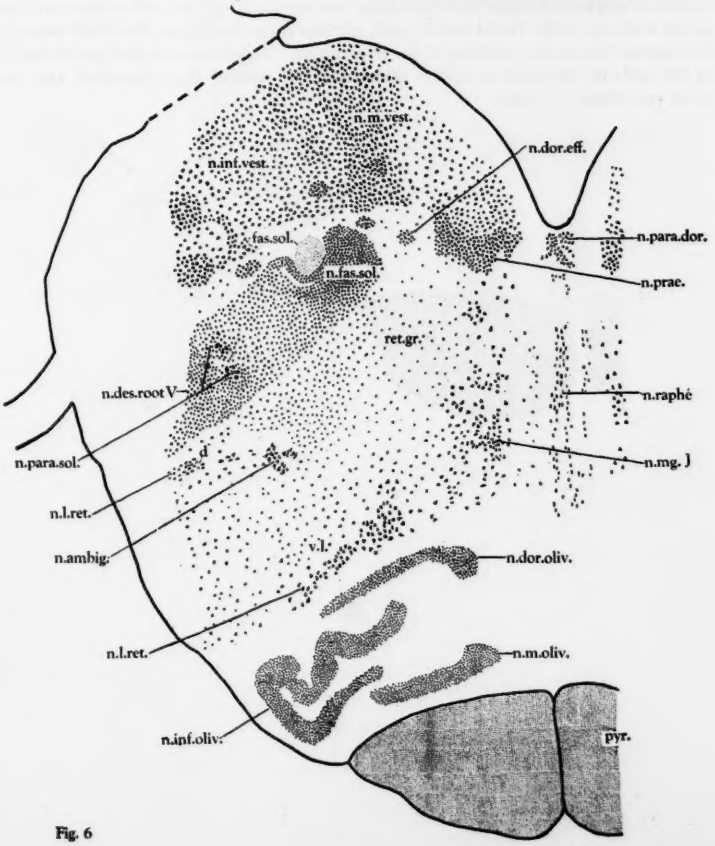
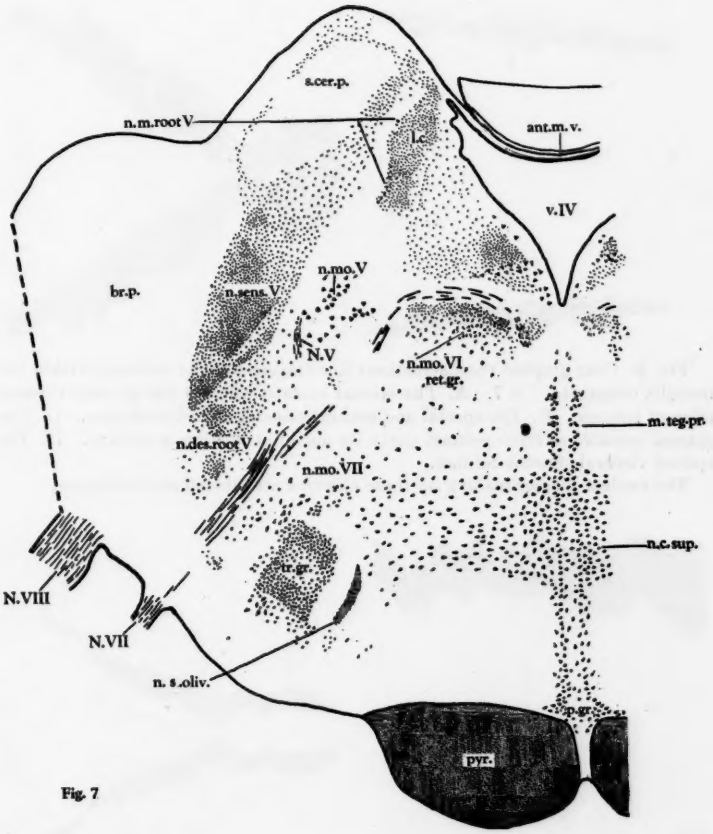

n.m.vest.
n.dor.eff.
n.inf.vest.
n.para.dor.
fas.sol.
n.fas.sol.
n.prae.
ret.gr.
n.des.root V
n.raphé
n.para.sol.
d
n.mg. J
n.l.ret.
n.ambig.
v.l.
n.dor.oliv.
n.l.ret.
n.m.oliv.
n.inf.oliv.
pyr.

Fig. 6

FIG. 7, This figure, although drawn from the same series as those illustrated in the preceding figures, because of the bend in the brain, is even more oblique, so that it shows ventrally the nucleus of the descending root and neurons of the motor nucleus of the facial nerve, and, farther dorsalward, are the chief sensory nucleus and the motor nucleus of the trigeminal. Attention is called particularly to the cells of the nucleus of the mesencephalic root of the trigeminal and the locus coeruleus. × 10.8.


s.cer.p.
n.m.root V
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ant.m.v.
v.IV
br.p.
n.mo.V
n.sens.V
N.V
n.mo.VI,
ret.gr.
m.teg.pr.
n.des.root V
n.mo.VII
n.c.sup.
r.gr.
N.VIII
N.VII
n. s.oliv.
p.gr.
pyr.

Fig. 7

FIG. 8. Four graphic reconstructions illustrating nuclear columns within the medulla oblongata. × 7. A. The special somatic efferent and general visceral efferent column. B. The special and general visceral afferent columns. C. The general somatic afferent column (only its medullar portion is shown). D. The special visceral efferent column.

The nuclear masses making up these columns are labeled on the figures.

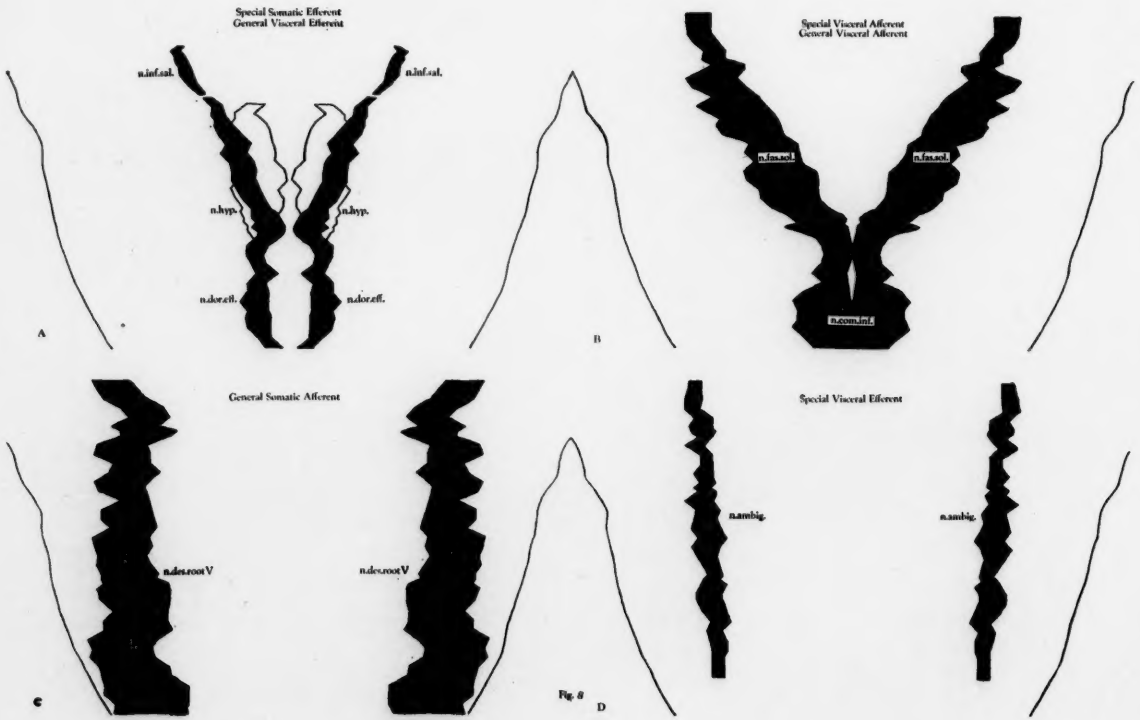
Special Somatic Efferent
General Visceral Efferent
n.inf.sal.
n.inf.sal.
n.hyp.
n.hyp.
n.dor.eff.
n.dor.eff.
A
Special Visceral Afferent
General Visceral Afferent
n.fas.sol.
n.fas.sol.
n.com.inf.
B
General Somatic Afferent
n.des.root V
n.des.root V
C
n.ambig.
Special Visceral Efferent
n.ambig.
D

Fig. 8

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